Ecohydrological drivers of Neotropical vegetation in montane ecosystems

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Short title: Ecohydrology of Neotropical montane ecosystems

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Abstract

Montane ecosystems are known for their high numbers of endemic species, unique climate conditions, and wide variety of ecosystem services such as water supply and carbon storage. Although many ecohydrological and climatic studies of montane environments have been carried out in temperate and boreal regions, few have been done in Neotropical regions. Hence, the objective of this review is to synthesize the existing literature on the main factors (biotic and abiotic) that influence vegetation distribution, functional traits, and ecohydrological processes and feedbacks in tropical montane ecosystems (TME) and to identify key knowledge gaps. Most of the literature used includes work conducted in Neotropical montane rainforests, cloud forests, and grass/scrublands (e.g., *páramos, punas,* and *campos de altitude/rupestres*). Fog is a major climatic attribute in tropical montane habitats. We found that fog regimes (frequency and intensity of fog events) influence both water inputs (i.e., canopy interception, foliar water uptake) and outputs (evapotranspiration), and represent an important driver of local species composition, dominance of plant functional types, and ecological functioning. The stability and conservation of TME depends on such ecohydrological fluxes, which are sensitive to increases in air temperature and changing precipitation and fog regimes. Furthermore, to better inform effective conservation and restoration strategies, more work is needed to elucidate how key ecohydrological processes are affected by land use conversion to agriculture and pasture lands, as human activities influence the water budgets in Neotropical montane watersheds not only at regional-scales, but also globally.

Keywords: cloud forest, montane rain forest, grasslands, fog, water and carbon budgets, ecosystem services, ecophysiology.

1. Introduction

Tropical mountain regions are known for their rich species diversity and high endemism (Myers *et al.*, 2000). These regions provide many ecosystem services, such as the maintenance of water quality and water supply, protection against soil erosion, and carbon storage (Dias *et al.*, 2003; Nogués-Bravo *et al.*, 2007; Bruijnzeel *et al.*, 2011; Spracklen and Righelato, 2014). Their influence is not limited to their geographical boundaries, but extends to the surrounding lowlands, shaping watershed scale hydrologic and climatic regimes (Nogués-Bravo *et al.*, 2007; Dias *et al.*, 2003).

To date, previous efforts aimed at synthesizing the ecohydrology of tropical montane ecosystems have generally focused on the global extent of all montane ecosystems (e.g., Beniston, 2003) or exclusively on tropical montane forested ecosystems (e.g., Hamilton *et al.*, 1995). Comparative syntheses including tropical montane grassland and shrubland ecosystems (above treeline) are lacking in such studies, despite their recognized role in providing key hydrological services (Dias *et al.*, 2003; Nogués-Bravo *et al.*, 2007). Tropical montane ecosystems are considered especially susceptible to global climatic changes and land use conversion (Dias *et al.*, 2003), and consequently, ecohydrological processes on tropical mountains may exhibit a greater magnitude and faster rates of change in response to changes in environmental conditions than lower altitude forests (Gibbs *et al.*, 2010). Moreover, global warming rates have been shown to be especially pronounced at higher elevations, which could potentially accelerate the rate of change in hydrological regimes and biodiversity in tropical montane ecosystems (Pepin *et al.*, 2015).

Vegetation removal or conversion to other land uses may also alter ecohydrological processes in tropical montane ecosystems through decreases or increases in evapotranspiration,

changes in throughfall and soil moisture dynamics, variations in water input from fog, and altered infiltration and runoff response (Foster, 2001; Oliveira *et al.*, 2014a). Further, land use change often causes changes in soils hydro-physical properties (e.g., hydraulic conductivity and pore space size and distribution), which can alter nutrient turnover time and organic matter decomposition rate (Leon and Osorio, 2014). Combined, these impacts may affect the provisioning (e.g., water supply) and regulation (e.g., flood mitigation) of hydrological ecosystem services (Foster, 2001; Ponette-Gonzalez *et al.*, 2009). Developing countries, including most Neotropical countries, are experiencing the highest rates of land use change globally (Gibbs *et al.*, 2010).

The high sensitivity of tropical montane ecosystems to both climatic and anthropogenic changes has already resulted in significant modifications of their ecohydrological processes, including evapotranspiration, streamflow, infiltration, and runoff (Wohl *et al.*, 2012). Consequently, the need to enhance scientific understanding of the ecohydrological consequences of land use and climate change on tropical mountains as a basis developing effective strategies for mitigating their effects on ecosystem services is especially urgent. To this end, we conducted a comparative synthesis of the ecohydrological drivers of vegetation distribution, vegetation–water interactions, and ecohydrological feedback mechanisms for the dominant Neotropical montane forests and grass/scrublands ecosystems. Specifically, we address the following questions: (1) How do edaphic, climatic and hydrological characteristics of tropical montane landscapes affect the distribution and functional traits of vegetation? (2) How do plant traits and physiological functioning feedback to influence the ecohydrology of Neotropical montane ecosystems? (3) What are the possible effects of land use and climate change on Neotropical montane vegetation and their hydrological functioning? To address these questions, we searched

through nearly 200 studies from the existing literature, using the following key terms: montane vegetation, ecology, geology, meteorology, anthropogenic processes, TMRF, TMCF, *campos rupestres*, *campos de altitude*, *páramos*, and *punas*; and any approximate or related terms to ecohydrology and ecophysiology.

2. Edaphic, climatic, and hydrological controls on the distribution and functional traits of Neotropical montane ecosystems

In the Neotropics, where mountain regions extend above 6,000 m.a.s.l, elevation is a main driver of environmental conditions and variability, which gives rise to many different types of vegetation with distinct traits and functionalities (Figures 1, 2). Increasing elevation is associated with a decline in atmospheric pressure, temperature, evapotranspiration (ET), and photon flux density, and an increase in cloudiness, ultraviolet B (UV-B) radiation (Letts and Mulligan, 2004), relative humidity, and annual rainfall (Hamilton *et al.*, 1995; Gerald *et al.*, 2008) (Table 1). Neotropical montane ecosystems can be broadly distributed into two major groups: (1) forest ecosystems, including tropical montane rainforests (TMRFs) and tropical montane cloud forests (TMCFs), and (2) grassland and scrubland ecosystems, including *páramos*, *punas*, "*campos de altitude*" (altitudinal grasslands), and "*campos rupestres*" (rock outcrop grasslands/scrublands or mountaintop grasslands). However, the specific combination of factors leading to a particular vegetation type is poorly defined for tropical montane systems. Moreover, the high degree of altitudinal and climatic overlap (Table 1) among these ecosystems underscores the need for better delineation of the environmental determinants of their establishment and persistence. In this section, we synthesize the current understanding of the

distinct climatic, edaphic and hydrological characteristics that influence the species distribution and the functional traits of each of these tropical montane ecosystems.

2.1. Tropical montane forests

Relative to temperate montane forests, tropical montane forested ecosystems have a more constant temperature and higher relative humidity, even during the "dry season," which typically is less pronounced (>100 mm month^{-1} is typical for dry periods). TMRFs and TMCFs are particularly distinct from lowland tropical forests in regard to their carbon and water budgets. For example, Gotsch *et al.* (2016) found that microclimatic factors (e.g., energy-limitation) of high altitude forests suppressed photosynthetic rates, which resulted in a lower net productivity and transpiration, but higher water use efficiency than lowland forests. Meanwhile, TMRFs are characterized by high precipitation inputs (3,000–8,000 mm year^{-1}) with negligible fog contributions (Holdridge, 1967), while TMCFs receive between 800-3,400 mm year^{-1} and are frequently covered in clouds or mist (Jarvis and Mulligan, 2011). The persistent fog typical of TMCFs and associated wet and cool climate distinguishes them from other terrestrial ecosystems (Still *et al.*, 1999, Jarvis and Mulligan, 2011).

Comparing the soil of different montane forests, TMRFs soils generally have higher nutrient availability than those of TMCFs, especially phosphorous (P) and nitrogen (N) (Wilcke *et al.*, 2001; Graefe *et al.*, 2010). This is due to lower temperatures and higher soil water saturation with elevation that decreases mineralization rates (Gerald, 2008). Some studies showed declining nutrient availability and increase in acidity as elevation increases (Homeier *et al.*, 2010; Wilcke *et al.*, 2002; Wilcke *et al.*, 2008; Bücker *et al.*, 2010), which results in a decrease of soil microbial activity and, thus, organic material decomposition rates (Bruijnzeel *et*

al., 2011). This slow organic matter decomposition in montane forests promotes an inverse relationship between P levels in the litter and soil (i.e. the higher the P levels in litter, the lower the P levels in soils) (Turner, 2004). The development of the organic horizon of TMRFs soils, which is substantially thicker than in TMCFs, provides more favorable conditions for plant growth (Wilcke *et al.*, 2002), while a large proportion of total nutrients is retained in the litter (Wilcke *et al.*, 2001). Moreover, the combination of climatic conditions and faster nutrient cycling results in a higher primary productivity and plant biodiversity in TMRFs compared to TMCFs (Clark *et al.*, 2015).

The vegetation in TMRFs is mostly composed of evergreen tree species (Moore, 2008), which vary greatly across regions. A notable feature of both TMRFs and TMCFs is the abundance of co-occurring plant functional types (PFTs; e.g., trees, palms, epiphytes, ferns, and herbaceous understory plants), with dicot trees comprising up to 80% of the forest stand (Lieberman *et al.*, 1996). Epiphytes are more common at the altitudes where fog is frequent and provides an important water source (Grubb and Whitmore, 1966, Grubb, 1974). As altitude increases, hemiepiphytes become more abundant and lianas less abundant (Hernandez *et al.*, 2012; Vazquez and Givnish, 1998, Jimenez-Castillo and Lust, 2013), while palms and lianas are more abundant in warmer TMRFs, where conditions are similar to those of their preferred lowland and premontane microclimates (Lieberman *et al.*, 1996). It is also notable that tropical conifers, although rare because of climatic and edaphic restrictions, are found in some TMRFs in Brazil (*Podocarpus* sp., *Araucaria* sp.) (Longhi *et al.*, 2010), Chile, and Argentina (*Araucaria* sp.) (Reis *et al.*, 2014), which can provide important ecohydrological functions. For example, *Araucaria* sp. provides shade to understory and midstory plants while still allowing a large amount of water to reach the soil and the inter-canopy atmosphere through weak interception and

stemflow (Thomaz and Antoneli, 2015), and has an important role in increasing soil nutrients through large litter inputs (Thomaz, 2007).

The transition between TMRFs and TMCFs is mainly determined by atmospheric and soil humidity levels, as well as the frequency and intensity of fog (Grubb and Whitmore, 1966, Bruijnzeel *et al.*, 2010, Mulligan, 2010, Jarvis and Mulligan, 2011). However, because of the highly variable environmental and topographical conditions on tropical mountains, there is no exact altitudinal transition between these two ecosystems (Table 1) (Richter, 2008). Moreover, because of the great diversity of PFTs and their dependence on local climatic conditions, it is not possible to categorize these ecosystems on the basis of plant species occurrence alone, and often structural characteristics are used to delineate vegetation distribution and functional traits. For example, in the transition from TMRF to TMCF ecosystems, there are significant changes in forest structure, including shorter and more multi-stemmed trees, declining presence of buttressed roots (Grubb, 1977; Lieberman *et al.*, 1996; Leuschner *et al.*, 2007; Richter, 2008; Soethe *et al.*, 2008; Wilcke *et al.*, 2008), increasing root–shoot ratio (Leuschner *et al.*, 2007) and root longevity (Graefe *et al.*, 2008), and thicker and more coriaceous leaves (Grubb 1977). These leaf adaptations not only provide protection from strong winds and high radiation, but also help drain water from their leaf surface, which is important since high leaf wetness caused by persistent fog or rain can suppress plant gas exchange (Aparecido *et al.*, 2017). Other leaf adaptive traits that help maintain gas exchange in high-altitude plants include: trichomes, water repellency (Holder, 2007; Rosado *et al.*, 2010; Aparecido *et al.*, 2017), and drip-tips (leaf drainage) (Malhado *et al.*, 2012; Goldsmith *et al.*, 2016). Additionally, some species can take advantage of these leaf wetness events by absorbing water directly though their leaves, which can alleviate the effects of periodic moisture stress on plant functioning (Hietz, 2010; Eller *et al.*,

2013; Goldsmith *et al.*, 2013, Gotsch *et al.* 2014).

The underlying drivers that alter vegetation structure along the transition from TMRFs to TMCFs with increasing altitude have been explored in great detail (Sanchez *et al.*, 2013; Hager and Dohrenbusch, 2011; Lieberman *et al.*, 1996; Kessler 2001; Vázquez and Givnish, 1998; Girardin *et al.*, 2014; Homeier *et al.*, 2010; Martin *et al.*, 2010; Prada and Stevenson, 2016; Clark *et al.*, 2015; Veneklaas and Van Ek, 1990). Yet, much uncertainty remains (Foster, 2001) and generalities are challenging to make (Bruijnzeel *et al.*, 2011). Several hypotheses put forth have emphasized the role of changing microclimate conditions with increasing elevation. For example, TMCFs have more acidic soils with low fertility, due to low decomposition and mineralization rates under wet and cold conditions (Bruijnzeel and Veneklaas, 1998), and lower energy inputs due to persistent fog and cloud, resulting in lower transpiration (T) and photosynthetic activity (Stadtmüller, 1987; Bruijnzeel and Veneklaas, 1998). TMCFs also are more prone to anoxic conditions due to soil saturation, which inhibits root respiration (Weaver *et al.* 1973; Bruijnzeel and Proctor, 1995; Bruijnzeel and Veneklaas, 1998). Other associated factors that differentiate TMRFs and TMCFs include greater soil toxicity with elevation due to higher aluminium saturation and lower pH (Hafkenscheid, 2000), strong winds, which can cause physiological desiccation (Bruijnzeel and Veneklaas, 1998); and high UV-B, which requires that plants maintain high levels of protective phenolic compounds in leaves. High UV-B may have detrimental effects on photosynthesis, stomatal opening, root cell division, and ion uptake (Bruijnzeel and Veneklaas, 1998; Foster, 2001), which further affects vegetation structure.

2.2. Grassland/scrubland montane ecosystems

Neotropical montane grasslands and scrublands include the Andean *páramos* and *punas*, which are grasslands dominated by megaphytic Asteraceae species (e.g., giant rosette plants) (Diaz *et al.*, 1997) (Figure 1e-j), and the Brazilian *campos rupestres* and *campos de altitude*, which are dominated by small sclerophyllous trees and shrubs interspersed in a matrix of grasses and sedges (Oliveira *et al.*, 2016). In this section, we further describe how the combination of elevation, latitude, and local climate interact to influence the distribution of these vegetation types, plant functional traits, and the transition between forest and grassland ecosystems.

Páramo ecosystems lie above the tree line and below the perpetual snow line, at altitudes ranging from about 3,000 to 4,500 m.a.s.l. (Baruch, 1984). They are found mainly in the northern Andes of Venezuela, Colombia, Ecuador, and Peru, and to a lesser extent in Central America (Nicaragua, Costa Rica, and Panama). They cover approximately 35,000 km^2 (Madriñán *et al.*, 2013) between latitudes 11 °N and 8 °S (Frantzen and Bouman, 1989).

Due to the high elevation, the *páramo* climate is typically cold and humid throughout the year, with frequent night frosts, strong winds, intense solar radiation, and high relative humidity, ranging between 70% and 90% (Luteyn, 1999; Buytaert *et al.*, 2011; Córdova *et al.*, 2015). Mean annual temperatures vary between 2-10 °C, decreasing with altitude, while diurnal temperature fluctuations are especially extreme, often varying by 20 °C (van der Hammen and Hooghiemstra, 2000). Climate and precipitation regimes vary depending on the geographical location of a particular *páramo* region with respect to (1) the position of the Intertropical Convergence Zone (Vuille *et al.*, 2000); (2) regional circulation patterns such as the El Niño Southern Oscillation (Martínez *et al.*, 2011); (3) the north-easterly Caribbean trade winds (Lauer, 1979); and (4) the Humboldt Current (Jørgensen *et al.*, 2011). Precipitation in the *páramo* is characterized by frequent rainfall, mainly in the form of drizzle (long duration, low intensity) (Padrón *et al.*,

2015). Annual rainfall amounts depend on the geographical location, with patterns that are difficult to generalize due to the complex topography of the Andean mountain barrier and the influence of water vapor stemming from both the Pacific Ocean and the Amazon basin (Vuille *et al.*, 2000; Garreaud, 2009). As a result, annual precipitation is highly variable (Luteyn, 1992) and can reach values as low as 500 mm (e.g., the dry *páramos* of Central Ecuador and Venezuela) and as high as >3,000 mm (e.g., the outer slopes in the Colombian western and eastern Cordillera; Buytaert *et al.*, 2011). Although fog is common in the *páramo*, with an estimated contribution of up to 35% of additional water inputs in an Ecuadorian TMRF- *páramo* transition zone (Bendix *et al.*, 2008; Rollenbeck *et al.*, 2011), detailed studies on the relative importance of fog to total water inputs and water balance are still lacking.

Geologically, the *páramo* is of relatively recent origin and consists of U-shaped valleys formed by glacial activity (Schubert, 1980; Coltorti and Ollier, 2000). The main soil types are Histosols and Andosols (Buytaert *et al.*, 2005a), originated from the accumulation of organic matter and volcanic ash from past volcanic activity combined with low temperatures and high environmental humidity (Podwojewski *et al.*, 2002; Poulenard *et al.*, 2004). Because of their high organic matter content (Buytaert *et al.*, 2005b) and porous structure with low bulk density, these soils are humic and acidic with high water-storage capacity (up to 90% volume) (Buytaert *et al.*, 2006).

The *páramo* vegetation consists of a combination of species that have adapted to the ecosystem's extreme climatic conditions, including grasses, evergreen herbs, shrubs, rosette plants, and scattered dwarf forests (Cleef *et al.*, 1983; Frantzen and Bouman, 1989). Grasslands are the dominant cover type (> 70%), composed of tussock grasses (commonly in the genera *Calamagrostis*, *Festuca,* and *Stipa*) and various species of the Cyperaceae family. Most of the

remaining land area is wetlands, composed of cushion plants (such as *Plantago rigida* Kunth, *Xenophyllum humile* (Kunth) V.A. Kunk, and *Azorella* spp.) (Ramsay and Oxley, 1997; Sklenar and Jorgensen, 1999). The dominant tree species in the *páramo* are in the genus *Polylepis* (Rosaceae), distributed primarily as small patches near the lower elevation *páramo* boundary (~3,000-3,200 m a.s.l.) and as scattered individuals along the entire *páramo* elevation range (Hensen *et al.*, 2012) and comprising a relatively small proportion of the landscape (< 5%, (Mosquera *et al.*, 2015). Although the ecology and plant diversity of the *páramos* have been studied in detail, the ecophysiological traits related to different plant species' hydraulic functions and their feedbacks and interactions with the hydrologic regime at the catchment scale remain poorly investigated. For example, while the capacity of plants to absorb fog water through their leaves as a mechanism to alleviate moisture stress has been widely documented across diverse ecosystems (Goldsmith *et al.*, 2013), the capacity for foliar water uptake among *páramo* species is not known. Additionally, the role of different *páramo* vegetation types in influencing the water balance via processes such as canopy cloud water interception (e.g., Holwerda *et al.* 2010), transpiration (e.g., Alvarado-Barrientos *et al.*, 2014), and hydraulic redistribution (Oliveira *et al.*, 2014b), represents another important knowledge gap.

Puna grasslands, categorized as the drier version of the *páramo,* are found at altitudes between 3,200–5,000 m a.s.l. throughout Peru, Bolivia, Chile and Argentina (Nicholson, 2011). Their position on the opposite side of the eastern orographic chain from the Amazon basin explains the markedly lower precipitation (Sarmiento, 1986). Peruvian *punas* are the most humid (1,000-2,000 mm $year^{-1}$), whereas Chilean-Argentinian *punas* are desertic (< 100 mm $year^{-1}$). The *puna* of the southern Andes is particularly arid and cold, with a long, intense dry season (e.g., in Bolivian *punas* winter temperatures reach -30 ^{o}C and rainfall is ~300 mm $year^{-1}$) (Mani,

1968, Sarmiento, 1986). Relative humidity ranges between 35-65% throughout the year (Mani, 1968, Nicholson, 2011). In contrast to the *páramos*, where approximately 70% of annual rainfall occurs in the rainy season, the drier *punas* are much more seasonal, concentrating up to 90% in rainy season (Sarmiento, 1986) and experiencing less frequent fog and snow (Nicholson, 2011). Dry *puna* winters last between 6-8 months (Nicholson, 2011), which combined with relatively low cloud cover (~20% during the summer and 50% during winter), result in higher annual insolation rates and more extreme temperature fluctuations compared to *páramo*. Average annual temperatures range between 9–11 ^{o}C, with frequent nighttime frosts and daytime temperatures increasing sharply (up to 30 ^{o}C) on sunny, dry days.

Puna vegetation is dominated by open grasslands with scattered patches of dwarf forest (Becerra and Bittencourt, 2007). The *puna* vegetation is further classified along a decreasing moisture gradient as: humid *puna*, arid *puna*, thorn *puna*, succulent *puna*, and desert *puna* (Mani, 1968). Similar to the *páramos*, the vegetation in *puna* consists of a combination of species adapted to the ecosystem's extreme climatic conditions. The vegetation is dominated by tussock-like grasses (Poaceae; e.g. *Poa*, *Festuca*) and sedge (Cyperaceae) species, although scattered shrubs of Asteraceae (e.g. *Baccharis*), Solanaceae (e.g. *Fabiana*), and dwarf trees (*Polylepis*) are also found (Baied and Wheeler, 1993). However, these vegetation groups have shown to be dependent on local water and thermal stresses (Bonaventura *et al.* 1995; Lambrinos *et al.*, 2006). In contrast to the cushion plants that dominate *páramos* wetlands, in a Chilean *puna*, Lambrinos *et al.* (2006) observed that cushion live forms were most abundant on xeric, rocky sites with low water retention and high solar radiation. On these xeric sites, cushion plants' large water storage capacity was valuable to maintain metabolic functioning during hot, dry days, as well as moderating extreme diurnal temperature fluxes by keeping the cells warm and turgid to

withstand nighttime frosts (Kleier, 2001). Shrubs and grasses growing on these sites with more favorable soil conditions (i.e., deep soils with few rocks and higher water and nutrient availability) did not express specialized adaptive traits for moisture stress. However, they were physiologically adapted to rapidly upregulate gas exchange processes in response to occasional pulses of favorable temperature and solar radiation conditions throughout the day. To better understand patterns of landscape distribution and to predict *puna* vegetation response to future climatic change, additional adaptive traits for coping with environmental extremes should be elucidated.

Campos de altitude, found in southeastern Brazil (Figures 1, 2) between 1,800 to 2,900 m.a.s.l. and geographically distributed along the mountain chains of the Serra do Mar and Serra da Mantiqueira, are cool-humid, mountaintop grasslands and shrublands, underlain by igneous and metamorphic substrates (Safford, 2007). The cool-humid climate of *campos de altitude* is dominated by subtropical and temperate influences (Safford, 1999). Precipitation ranges between 1,500-3,000 mm $year^{-1}$, increasing with elevation due to an orographic effect, and is seasonally distributed, with the rainy season typically occurring between November and March and the dry season (reaching < 50 mm $month^{-1}$ in some areas) between June and August (Safford, 1999). Average annual temperature ranges between 12-18 °C, depending on altitude. Frost events occur during the winter in some areas, such as Itatiaia National Park at 2,200 m.a.s.l., where frost occurs ~56 days per year (Safford, 1999).*Campos de altitude* soils are characterized as having shallow soils with significant horizontal and vertical variation, ranging from clayey to rocky outcrops, and varying greatly according to local-scale topographic features such as well-drained slopes or poorly-drained bogs (Oliveira *et al.*, 1983). The *campos de altitude* mountain chains are ancient landscapes, with a long history of erosion; consequently, they occur at lower

elevations than the younger Andean mountains of western South America (Safford, 1999; Safford, 2007), where *páramo* occur.

In the *campos de altitude*, the environmental filters that most strongly influence vegetation establishment include frequent frost, high solar radiation, shallow soils, and dry conditions (Scarano, 2009), resulting in a dominance of phanerophytes, hemicryptophytes, and geophytes (Safford, 1999). In general, vegetation distribution is controlled by local topography, the drainage network, and the distribution of soil types (Safford, 2007). Nurse plants, which are able to colonize the rocky surfaces with especially harsh environments, play a critical role in facilitating the establishment and persistence of other species (Scarano, 2002; Scarano, 2009). Information about distinct plant traits and functioning of the Brazilian *campos de altitude* is relatively scarce. The *campos de altitude* that occur adjacent to cloud forests can also benefit from occasional fog, with additional cloud water inputs potentially compensating for dry season moisture deficits (Safford, 1999; Eller *et al.*, 2016).

Campos rupestres are montane grasslands and scrublands characterized by a mosaic of fire-prone vegetation and rocky outcrops of quartzite, sandstone, or ironstone substrate, occurring between 900 m and 2,050 m.a.s.l., primarily along the "Espinhaço" mountain range in eastern Brazil (Silveira *et al.*, 2016). Including a few sparse, disconnected locations, the total estimated area of *campos rupestres* is 66,447 km^2, with much of their original area replaced by anthropogenic activities, such as agriculture (Fernandes *et al.*, 2014). In contrast to *páramo* and *campos de altitude*, the climatic regime in the *campos rupestres* is more strongly seasonal, with a marked dry season occurring in May–September. Along the Espinhaço Range, latitudinal differences account for decreasing total rainfall towards the north and decreasing mean monthly temperatures towards the south (Silveira *et al.*, 2016). The average precipitation is 1461 ± 308

mm year^{-1}, and monthly temperatures vary from 16.0 ± 2.1°C in winter to 21.2 ± 1.5°C in summer (wet season) (Silveira *et al.*, 2016). Fog can occur in *campos rupestres*, but there are no data quantifying its relative contribution to the local water balance or to the vegetation physiology. Soils in *campos rupestres* are relatively old, poorly developed, extremely leached, nutrient-impoverished (mainly in phosphorus and cations), and consequently, strongly influenced by the acid, chemically poor parent materials (Oliveira *et al.*, 2015; Silveira *et al.*, 2016).

Similar to the other grasslands, *campo rupestres* are dominated by grasses, sedges, herbs, rosettes and shrubs, especially from the Asteraceae, Cyperaceae, Eriocaulaceae, Poaceae and Velloziaceae families (Le Stradic *et al.*, 2015). Vegetation growth is strongly influenced by water availability and soil properties. During the dry season, the shallow soils dry out and vapor pressure deficit increases, creating more stressful conditions for plant growth and survival (Oliveira *et al.*, 2016), and favoring perennial plants with very slow growth rates. *Campos rupestres* show the greatest degree of seasonality in precipitation among tropical montane ecosystems and, in this environment, plants use a wide range of strategies to cope with drought (Oliveira *et al.*, 2016). These plants have morphological and physiological adaptations to improve water and nutrient acquisition, including drought-tolerant, drought-avoiding, and desiccation-tolerant strategies (Porembski and Barthlott, 2000, Jacobi *et al.*, 2007, Oliveira *et al.*, 2016, Castro *et al.*, 2017, Vitarelli *et al.*, 2016). Drought-tolerant species in *campos rupestres* deal with drought by maintaining metabolism and cell turgor through regulatory mechanisms, such as strong stomata control over water loss. Drought-avoiding plants typically have deep or dimorphic root systems that enable them to access deep and stable water sources, or phenological strategies such as drought-decidousness (Brum *et al.*, 2017). Desiccation-tolerant plants enter an apparent anabiosis state resulting in a desiccated appearance. C*ampos rupestres* are particularly a

center of diversity for desiccation-tolerant vascular plants, also known as resurrection or poikilohydric plants, which are able to equilibrate their water content with that of dry air during water-limiting conditions (Porembski and Barthlott, 2000; Gaff and Oliver, 2013; Alcantara *et al.*, 2015).

Campos rupestres support one of the highest levels of plant biodiversity on Earth. For instance, about 1,590 species were recorded in a 200 km² area (Giulietti *et al.*, 1987). Species distribution in *campos rupestres* is also shaped in part by fire (Bush *et al.*, 2015; Safford, 2007), which could be critical to maintain plant diversity and the distinct plant community characteristics of these systems. Fires are mainly caused by lightning strikes at the transition between dry to rainy season and, hence, are closely coupled with the carbon and hydrological balance due to the large accumulation of dry fuel loads (Oliveira *et al.*, 2016).

3. Ecohydrological feedback mechanisms: How do vegetation characteristics influence hydrological processes in Neotropical mountains?

Across diverse ecosystems, plant species exhibit unique adaptive traits and functions that reflect a close coupling with the climatic conditions under which they have evolved (Foster, 2001; Jarvis and Mulligan, 2011; Oliveira *et al.*, 2014b). Because of this close coupling, Neotropical montane ecosystems not only respond to changing climatic conditions but also influence the local and regional climate through the interactions and feedbacks between vegetation and hydrology, including soil water infiltration and storage capacity, evapotranspiration, plant water storage, and fog-plant interactions. In this section, we discuss each of these ecohydrological processes in relation to the unique characteristics of each Neotropical montane ecosystem, as well as the larger-scale implications for water balance and

watershed hydrology.

3.1. Soil water infiltration and storage capacity

Differences in soil, vegetation, and climate are associated in multiple ways with differences in hydrological processes along altitudinal gradients. Neotropical montane ecosystems are located at the headwaters of watersheds that are the primary water supply to major population centers within lower-lying regions (Dias *et al.*, 2003; Soares *et al.*, 2012; Pinto *et al.*, 2015), including the Amazon river which alone delivers 18% of all fresh water to oceans globally (Subramaniam *et al.* 2007). Consequently, vegetation-climate interactions and feedbacks play a critical role in determining soil water inputs and storage capacity, especially by maintaining good soil-water transmissivity (i.e. the extent to which soil can transmit water through its entire saturated thickness). Such transmissivity, in turn, facilitates water recharge to groundwater aquifers, which further helps regulate discharge (Soares *et al.*, 2012; Pinto *et al.*, 2015). For example, closed-canopy forests such as TMRFs and TMCFs, typically maintain relatively high soil infiltration capacity, low runoff, high stemflow, and high soil moisture recharge, which combined, contribute to large total water inputs into the soil (Figure 4 – Bruijnzeel *et al.*, 2011, Teale *et al.*, 2014; Motzer *et al.*, 2005**;** Bruijnzeel *et al.*, 2011).

In all four grassland and scrubland environments discussed here, the soils tend to have high water storage capacity (Figure 4), associated with vegetation with dense roots to maintain soil stability. Consequently, in both Neotropical montane forests and grasslands, maintaining high soil-water transmissivity and storage represents an important ecohydrological function of the natural vegetation, which in turn, helps regulate the hydrological cycle, control erosion, and maintain high water quality at watershed scales (Foster, 2001). Changes in vegetation type and

abundance in many tropical montane ecosystems, often linked to changes in soil properties, could lead to negative consequences for water resource availability (Asdak *et al.*, 1998 Garcia-Coll, 2002).

For example, in the northern Andean *páramos*, water balance is largely determined by the marked topography-soil-vegetation conditions of the landscape (Mosquera *et al.*, 2015). Andosols with low bulk densities (~0.40 gr cm^{-3}) and high water retention capacities at saturation (~0.70 cm^3 cm^{-3}), mainly found in steep hillslopes with grassland vegetation, control the ecosystem's water regulation capacity (i.e. year-round sustainability of streamflow) via downslope subsurface drainage of water through these soils' porous matrix towards the soils at the valley bottoms. Relative to Andosols, Histosols have even lower bulk densities (< 0.3 gr cm^{-3}) and higher water retention capacities at saturation (> 0.80 cm^3 cm^{-3}), and are mainly found in wetland areas (at valley bottoms and flat hilltops) dominated by cushion plants that contribute to the high water storage capacity of the *páramo* (Mosquera *et al.*, 2016a; Mosquera *et al.*, 2016b).

3.2. Evapotranspiration

In Neotropical montane environments, evapotranspiration (ET) rates decrease with altitude in response to increasing cloud and fog cover, lower air temperatures, higher relative humidity, low incidence of net radiation, and high leaf wetness (Aparecido *et al.* 2016). In TMRFs, where precipitation rates are almost twofold greater than lowland tropical forests, ET and T are lower (between 800 and 1,300 mm $year^{-1}$, respectively), with T being equivalent to 30%~50% of ET (Bruijnzeel *et al.*, 2011; Good *et al.*, 2017). In TMCFs, which are cooler and wetter than TMRFs, the fraction of transpiration is usually lower (Bruijnzeel *et al.*, 2011). In

low-altitude forests (premontane and lowland forests), T can exceed 1,000 mm year^{-1} and the T/ET ratio can be over 50%. Consequently, transpiration from lowlands and premontane forests usually contributes more to the water balance compared to evaporation, because roots are able to tap into groundwater and soil-water reservoirs in addition to higher vapor pressure deficits, making the proportion of T in the overall ET flux very high (Jasechko *et al.*, 2013; Gotsch *et al.*, 2016).

In altitudinal grasslands, such as the ones found in the Mantiqueira mountains of Brazil, the mean annual potential evapotranspiration of a TMCF region is about 2.3 mm day^{-1} higher (~1,670 mm year^{-1}) than at the adjacent *campos de altitude* (~850 mm year^{-1}) (Eller *et al.*, 2015). In the *campos de altitudes* located in the Itatiaia National Park, ET is 660.9 ± 51.3 mm year^{-1}. In this system, the lowest ET rates occur during the hot and rainy season (average of 119.6 mm), from December to February, when precipitation input is high (1,147 mm) (Aximoff *et al.*, 2014). The lower ET of *campos de altitude* plays a major role in sustaining the higher soil water storage and associated springs in these ecosystems. Estimated ET in wet *páramo* watersheds in southern Ecuador (510 ± 49 mm yr^{-1}) is similar to that of *campos de altitude* (Mosquera *et al.*, 2015). Relatively low ET rates, combined with almost daily rainfall (mostly in the form of drizzle (Padrón *et al.*, 2015)) and high water infiltration and retention capacity (Buytaert *et al.*, 2006) of the *páramo* soils, leads to high water storage capacity (Mosquera *et al.*, 2015).

3.3. Vegetation water storage

Although plant species with specialized aboveground structures for water retention can be found in lower-altitude TMRFs (Holscher *et al.*, 2004; Hietz, 2010), the number and

importance of these adaptive strategies is apparently much higher in TMCFs (Veneklaas and Van Ek, 1990). For example, epiphytes (bromeliads, mosses, and lichens), which are especially abundance in TMCFs, intercept and uptake substantial amounts of water (Van Stan and Pypker, 2015; Holwerda *et al.*, 2010; Muñoz-Villers *et al.*, 2012; Veneklaas and Van Ek, 1990). During the wet season, bryophytic epiphytes are able to store, on average, up to 300% of their dry weight as water (Kohler *et al.*, 2007; Holscher *et al.*, 2004; Stanton *et al.*, 2014), while other type of epiphytes are able to store water in succulent tissues coupled with thicker cuticles that inhibit water loss (Gotsch *et al.*, 2015). Holscher *et al.* (2004) found that epiphytes contributed 6% of total canopy interception at a TMRF, with TMCFs likely to exhibit greater canopy fog interception due to a greater epiphyte abundance and fog immersion frequency. Quantifying interception by epiphytes in these ecosystems is challenging due to little knowledge of the rates in which water is taken up and lost under varying field conditions and specific epiphytic functional traits (Veneklaas and Van Ek 1990). Although water storage is vital for epiphytic growth and microclimate conditions (Stanton *et al.*, 2014)), some studies warn that potential interception among certain epiphytic functional groups (e.g., bryophytes) may result in less water and solutes reaching the forest floor during dry seasons, thus less water available for the host plants (Van Stan and Pypker, 2015; Fleischbein *et al.*, 2005; Ponnette-Gonzalez *et al.*, 2010).

In many Neotropical grassland and scrubland mountain ecosystems, rosettes are a prevalent life form (Figure 3). For example, *Espeletia* rosettes are an important genus in *páramos* (Asteraceae, Figure 3), rosettes from the families Asteraceae and Bromeliaceae are common in *campos de altitude*, and rosettes in the Velloziaceae (Figure 3), Eriocaulaceae, Asteraceae families occur in *campos rupestres*. Their presence provides useful insights about ecohydrological drivers that favor grasslands and shrublands over forests. The manner in which

the leaves are arranged in a terminal rosette is very important to the plant's physiological functioning, influencing its water and carbon acquisition capacity (Monasterio and Sarmiento, 1991). Rosettes and other herbaceous plants intercept and channel rainfall, essentially acting as funnels or channels that collect and direct significant proportions of total rainfall towards the layer of dead leaves. Water then flows through this layer to reach the base of the trunk, where a thick layer of roots with mycorrhizae associations are concentrated, facilitating rapid uptake of water and solutes (Monasterio and Sarmiento, 1991; Perez and Frangi, 2000). Similarly, Velozia spp. and Croton spp., which occur in *campos rupestres*, are able to collect water through stems and adventitious roots (Oliveira *et al.*, 2005), and via foliar water uptake (Vitarelli *et al.*, 2016). Hence, all these mechanisms can be very important to the water balance in *páramos* (e.g., *Espeletia*; Monasterio and Sarmiento, 1991) and in *campos rupestres* (e.g., *Vellozia* [Oliveira *et al.*, 2005; Alcantara *et al.*, 2015]), which are strongly affected by extreme diurnal and seasonal fluctuations in soil moisture availability and atmospheric demand.

3.4. Fog-vegetation interactions

As mentioned previously, fog plays an important role in the hydrology and productivity of tropical montane ecosystems (Célleri and Feyen, 2008; Goldsmith *et al.*, 2013) (Figure 4), and is considered a strong indicator of changes in plant diversity and functioning among different ecosystems. Not only does fog act as an extra water input (Muñoz-Villers *et al.*, 2012), it also limits water loss driven by high evaporative demand and solar radiation intensities, which are especially important during dry periods in seasonal cloud forests (Eller *et al.*, 2013; Oliveira *et al.*, 2014b; Gotsch *et al.*, 2015). Combined with the lower transpiration rates and higher canopy

fog interception in TMCFs compared with TMRFs (Gotsch *et al.*, 2016), these additional water inputs contribute to groundwater recharge and the regional streamflow (i.e., 9% from fog deposition in a *puna* grassland; Clark *et al.*, 2014), and enhance throughfall through "fog drip" (i.e., intercepted water running off the canopy leaves) (Figure 4 − Foster, 2001; Oliveira *et al.*, 2014).

Plant species in TMCFs tend to exhibit more prominent and diverse strategies for benefiting from leaf wetness compared to in TMRFs. For example, cuticle properties that promote water repellency can vary widely among species and, as a result, can be highly sensitive to environmental change (Oliveira *et al.*, 2014b). The greater amount of additional fog input in TMCFs compared to TMRFs (Figure 4) may also contribute to a higher occurrence of sap flow reversal, leading to greater amounts of foliar water uptake (FWU) (Goldsmith *et al.* 2013, Eller *et al.*, 2015). Indeed, FWU has been shown to contribute to 9% of the water lost through transpiration during dry seasons (Gotsch *et al.*, 2014). Hence, fog can be an important source of water for some plants that do not have a very strong stomata control and could reach hydraulic thresholds that might damage their hydraulic pathways (Eller *et al.*, 2016). Thus, some species are able to redistribute water taken in via their leaves or through roots and soil promoting tissue hydration, which enables and optimizes physiological processes during drier seasons (Eller *et al.*, 2015). Although TMRFs would benefit most from FWU due to its reduced soil water availability compared to TMCF, Goldsmith *et al.* (2013) argue that less frequent fog events most likely lead to fewer plant species developing this specialized trait. Additionally, the higher abundance of epiphytes capable of performing FWU in TMCFs is much higher, which consequently will result in a larger water source (e.g., 37-100% recovery from dry season transpiration; Hager and

Dohrenbush, 2011) for these ecosystems.

Taking in consideration the importance of foliar uptake of fog water, we would assume that this feature would be especially prevalent in altitudinal grassland species; however, there are no known studies that have documented FWU in tropical grassland and shrubland ecosystems. As cited previously, plants that occur at those altitudes and conditions (e.g., cold, windy, high solar radiation incidence, and precipitation input) have adapted various traits to collect and store precipitation water. Buytaert *et al.* (2011) gathered that fog frequency, constant cloud cover and high relative humidity suppresses transpiration, while low temperatures reduce overall evapotranspiration. Additionally, the drainage of fog water through the soil has shown to be a significant contributor to highland streamflow (Clark *et al.*, 2014); although less vegetated (or less specialized), shallow soil sites have resulted in an increase of runoff (Buytaert *et al.*, 2007).

4. Predictions and implications: threats from land use and climate change

Tropical mountain ecosystems worldwide are highly vulnerable to climatic and land use changes because of their limited and discontinuous geographical distribution, restricted altitudinal range, adaptation to unique climatic conditions, and large numbers of endemic species (Assis and Mattos, 2016). As a result, they are likely to be the first regions on the planet affected by such changes (Spehn *et al.*, 2006), and thus, can be considered as "early indicators" of climate change. The vulnerability of montane ecosystems can be mainly attributed to their dependence on distinct biotic and abiotic factors that are not always present in lowland forests, such as: 1) reliance on fog events as a water source, which increases with altitude; 2) adaptation to lower temperatures and vapor pressure deficit (i.e., higher susceptibility of plants to cavitation); and 3)

limited nutrient availability that might exacerbate with increase of runoff and reduction of microbial activity. Below, we further discuss these three factors in the context of increase of land cover change in the Neotropics and global trends of a changing climate.

Although Neotropical mountains are relatively less-affected by agricultural practices than their surrounding lowlands, they are highly impacted by other land use conversion practices such as deforestation, road construction, fire, invasion of non-native species, and mining activities (Bubb *et al.*, 2004). However, activities that occur in lowland forests also have an indirect effect on montane ecosystems. Extensive deforestation in lower altitudes (from lowland to TMRFs) not only reduces rainfall locally, due to reduced rain recycling (Pielke *et al*., 2007), but also result in lower moisture outputs to higher altitudes, which leads to lower fog frequency (Lawton, 1984).

Anthropogenic practices can also affect soil and stream water chemistry (Bücker *et al.*, 2011), increase surface runoff, and reduce soil water retention capacity, leading to more frequent flood events (Célleri and Feyen, 2008). For instance, expansion of road systems and degraded pastures, croplands, and mining fields in mountain ecosystems can cause slope instability, which increase the frequency of landslides. Landslides cause loss of nutrient and soil horizons, reduced infiltration, and lower water storage capacities (Restrepo *et al*., 2009). Although increases in runoff associated with anthropogenic activities might enhance water supplies to nearby streams and springs, this effect is only temporary. When rainfall ceases, these streams face reduced flows during dry periods leading to less water availability to flora, fauna and local populations. Additionally, larger floods alter sediment regimes. Higher rainfall areas such as TMRFs are likely to experience the largest ecohydrological changes associated with anthropogenic activity.

In altitudinal grassland ecosystems, however, land use change, which mainly involves livestock grazing, periodic natural and/or manmade fires, agriculture, reforestation, fish farming,

mining, and mineral extraction, have resulted in other drastic types of soil degradation (Luteyn, 2005). Over the last 100 years, these ecosystems have undergone large-scale and often extreme landscape transformations into agricultural lands and human settlements (IUFRO, 2000), which fragmented and isolated the remnant *páramos*, making them more vulnerable to climatic changes (Buytaert *et al.*, 2014). Compaction due to livestock grazing and loss of vegetative cover promotes drying of the soils, which irreversibly reduces their pore space and water-holding capacity (Poulenard *et al.*, 2003). Such disturbances can also cause soils to become crusted and hydrophobic, dramatically reducing their normally high water retention and regulation capacity (Poulenard *et al.*, 2001). *Campos rupestres* and *campos de altitude* are greatly threatened as well, mainly by natural resource exploitation, especially, mining in the past for gold and diamonds, and more recently for iron (Assis and Mattos, 2016). Reduced soil water retention is likely to increase vulnerability of these ecosystems to climate change.

Although deforestation can be the major culprit for microclimatic changes and ecosystem degradation, the intensification of global warming (i.e., climate change) has shown to exacerbate these effects in montane ecosystems. Climate change scenarios for mountain regions predict an increase in surface temperatures and changes in precipitation regimes, in which extreme events (i.e., drought, fire, frost and storms) may become more frequent and of greater magnitude (IPCC, 2014). Along with the documented upward migration of plant and animal species, tree mortality in Neotropical forests has increased due to recurring drought events and associated wildfires (Sherman *et al.*, 2008). Given the low frequency of fire in all but the driest tropical montane ecosystems and poor adaptations to drought in the wetter sites, these ecosystems are particularly vulnerable to more extreme fire and drought-related mortality (Oliveras *et al*., 2013).

Soil water availability and atmospheric vapor pressure deficit are considered the main

environmental drivers that influence plant responses to drought, especially regulating plant gas exchange (Cernusak *et al.* 2007). In the case of mountain species, evidence suggests that gas exchange is reduced in response to drought events (Damour *et al.*, 2010; Brum *et al.*, 2013; Eller *et al.*, 2015; Brum *et al.*, 2017). Montane plants acclimated to less extreme climate conditions are at risk to exceed cavitation thresholds under future drought conditions (Damour *et al.* 2010, Schuldt *et al.* 2011) and experience irreversible cavitation, which consequently leads to significant reduction in transpiration rates, productivity and, ultimately, mortality (McDowell *et al*., 2008; Bonal *et al.*, 2016).

Furthermore, climatic models indicate substantial reduction in fog frequency in mountain regions. As stated previously, montane vegetation at every altitudinal belt are dependent on fog events to some extent. However, among the mountain ecosystems studied, TMCF might suffer more intensely from the reductions in fog quantity and frequency. The vulnerability of TMCF under climate change scenarios has been predicted by Ponce-Reys *et al.* (2012) which estimated a 68% loss of climatically suitable habitat for Mexican cloud forests by 2080, making it one of the most vulnerable ecosystems in the world to short-term climate change impacts. These climatic models also suggest that climate change has brought about a reduction in low-altitude cloud formation in TMCFs (Foster, 2001; Still *et al.*, 1999). Reduced cloud cover not only reduces vegetation composition, but precipitation and fog frequency are lower and surface evaporation is higher, which results in decreased streamflow (Bruijnzeel and Scatena, 2011).

At the plant level, studies have shown that reduction in fog frequency can lead to plant tissue desiccation, which might ultimately result in mortality and associated lower canopy interception rates and storage capacities (Foster, 2001). Increased plant mortality in these ecosystems will ultimately result in long-term microclimatic changes that will affect the

succession rates (due to slower growth rates as altitude increases) and plant composition (e.g., more fast growing plant species, such as grasses, than trees and shrubs; in addition to more adapted invasive species). Potentially cascading effects of such microclimatic changes from less fog and vegetation cover include higher radiation incidence, higher vapor pressure deficits and higher temperatures (air and leaf), which can intensify the drought condition and, consequently, can further increase plant mortality.

Additionally, as climate change leads to temperature increases worldwide and longer recovery times (especially for the tropics; Schwalm *et al.*, 2017), mountain ecosystems are likely to continue "migrating" upwards. This effect could lead to disappearance of some tropical montane ecosystems as they are often located at the top of mountain ranges (Still *et al.*, 1999, Bubb *et al.*, 2004); while also favoring the introduction of highly resource-competitive, invasive plant species that will likely suppress local plant communities (Foster, 2001). The combination of microclimatic changes induced by climate change and land use conversions also increases the susceptibility of these ecosystems to the invasion of exotic plant species, which may use significantly larger amounts water than their native counterparts (Cavaleri *et al*., 2014), further altering the ecohydrologic processes in these ecosystems.

Altered hydrologic cycles associated with ecosystem degradation in montane systems can also indirectly affect the ecosystem functioning of lower altitude forests, and urban areas that rely on a constant supply of water. Hence, about a more mechanistic understanding of soil-plant-water interactions these ecosystems is vital to predict and, especially, to mitigate the effects of climate and land use change in Neotropical montane ecosystems and preserve their unique biodiversity and ecosystem services.

5. Concluding remarks

We highlight the interactions that operate within the soil–vegetation–atmosphere continuum unique to Neotropical montane ecosystems, whose feedbacks can lead to dramatic effects on the water supply to lower altitudes (soils and streams), prolonged droughts, and an increase in natural disasters, such as landslides and wildfires that ultimately change the biodiversity of these ecosystems. The need is therefore urgent for further study of the existing plant species and how they function individually and as a community, and for experiments to evaluate the ecohydrological and physiological resiliency of these ecosystems (e.g., soil water recharge capability at various elevations affected by plant coverage). In particular, knowing the primary determinants of each plant community structure and function is paramount to predict how these ecosystems will shift under future climate scenarios. Experiments and observations that cover broad altitudinal gradients, especially those that span plant types, altitudinal gradients, and climates, would greatly improve our understanding of Neotropical montane ecosystems. Such studies would provide the accurate scientific information that is critical for developing better management and conservation strategies to help sustain these tropical montane regions and their valuable ecosystem services.

Finally, it is worth noting that although the ecosystem services provided by mountainous systems worldwide are well recognized, our current inadequate knowledge of these regions is largely because of the difficulty of conducting research in such remote and often inhospitable locations. While this study contributes to our understanding of how plant and ecosystem functioning is differentiated among the various types of tropical montane ecosystems, more work

is needed to fully identify the mechanisms that determine the development of *páramos*, *punas, campos rupestres*, and *campos de altitude* vegetation communities and their interface with forested ecosystems at lower altitudes. We especially need to further describe the contribution of fog to plants metabolism and water balance and plant strategies to cope with the climatic conditions in order to preserve them in the future. Such knowledge is essential to develop models that can help predict how global change drivers will ultimately affect the eco-hydro-physiological functioning in these important ecosystems.

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7. References

Alcantara, S., Mello-Silva, R., Teodoro, G. S., Drequeceler, K., Ackerly, D. D. and Oliveira, R. S. 2015. Carbon assimilation and habitat segregation in resurrection plants: Comparison between desiccation and non-desiccation tolerant species of Neotropical Velloziaceae (Pandanales). *Functional Ecology* **29:** 1499-1512.

Alvarado-Barrientos, M. S., Holwerda, F., Asbjornsen, H., Dawson, T. E. and Bruijnzeel, L. A. 2014. Suppression of transpiration due to cloud immersion in a seasonally dry Mexican weeping pine plantation. *Agricultural and Forest Meteorology* **186:** 12-25.

Ammondt, S. A. and Litton, C. M. 2011. Competition between Native Hawaiian Plants and the Invasive Grass Megathyrsus maximus: Implications of functional diversity for ecological restoration. *Restoration Ecology* **20 (5):** 638-646.

Aparecido, L. M. T., Miller, G. R., Cahill, A. T. and Moore, G. W. 2016. Comparison of tree transpiration under wet and dry canopy conditions in a Costa Rican premontane tropical forest. *Hydrological Processes* **30 (26):** 5000-5011.

Aparecido, L.M.T.; Miller, G.R.; Cahill, A.T.; Moore, G.W. 2017. Leaf surface traits and water storage retention affect photosynthetic responses to leaf surface wetness among wet tropical forest and semiarid savanna plants. *Tree Physiology* **37(10):**1285-1300.

Asbjornsen, H., Velázquez-Rosas, A., García-Soriano, R., Gallardo-Hernández, C. 2005. Deep ground fires cause massive above- and below-ground biomass losess in tropical montane cloud forests in Oaxaca, Mexico. *Journal of Tropical Ecology* **21:** 427-434.

Asdak, C., P. Jarvis, P. Van Gardingen, and A. Fraser. 1998. Rainfall interception loss in unlogged and logged forest areas of Central Kalimantan, Indonesia. *Journal of Hydrology* **206 (3):** 237-244.

Assis, M. V. and Mattos, E. A. 2016. Vulnerabilidade da vegetação de campos de altitude às mudanças climáticas. *Oecologia Australis* **20:** 24-36.

Aximoff, I. A., Alves, R. G. and Rodrigues, R. C. 2014. Campos de altitude do Itatiaia: aspectos ambientais, biológicos e ecológicos. Brasilia, Brazil, Ministério do Meio Ambiente. **Boletim número 18**.

Baied, C.A. and Wheeler, J.C. 1993. Evolution of high Andean puna ecosystems: environment, climate, and culture change over the last 12,000 years in the central Andes. *Mountain Research and Development* **13(2):** 145-156.

Baruch, Z. 1984. Ordination and classification of vegetation along an altitudinal gradient in the Venezuelan Paramos. *Vegetation* **55 (2):** 115-126.

Becerra, J. A. B. and Bittencourt, M. D. 2007. Ecological zoning of an Andean grasslands (puna) at the Manu biosphere reserve, Peru. *International Journal Environment and Sustainable Development* **6 (4):** 357-372.

Bendix, J., R. Rollenbeck, M. Richter, P. Fabian, and P. Emck. 2008. Climate. *Gradients in a Tropical Mountain Ecosystem of Ecuador.* E. Beck, J. Bendix, I. Kottke, F. Makeschin, and R. Mosandl (eds). Springer, Berlin: 63–73.

Beniston, M. 2003. Climatic change in mountain regions: a review of possible impacts. *Climatic change* **59(1-2):** 5-31.

Bivand, R., Lewin-Koh, N. 2017. Maptools: Tools for Reading and Handling Spatial Objects. R package version 0.9-2. Available online at: https://CRAN.R-project.org/package=maptools.

Bonal, D., Burban, B., Stahl, C., Wagner, F. and Herault, B. 2016. The response of tropical

rainforests to drought - lessons from recent research and future prospects. *Annals of Forest Science* **73:** 27-44.
Bonaventura, S.M., Tecchi, R., Vignale, D. 1995. The vegetation of the puna belt at Laguna de Pozuelos biosphere Reserve in northwest Argentina. *Vegetatio* **119:** 23-31.
Bruijnzeel, L. A., Kapelle, M., Mulligan, M. and Scatena, F. N. 2010. Tropical montane cloud forests: state of knowledge and sustainability perspectives in a changing world. *Tropical Montane Cloud Forests: Science for Conservation and Management*. L. A. Bruijnzeel, F. N. Scatena and L. S. Hamilton (eds). Cambridge University Press, Cambridge, UK**:** 691-740.
Bruijnzeel, L. A., Mulligan, M. and Scatena, F. N. 2011. Hydrometeorology of tropical montane cloud forests: emerging patterns *Hydrological Processes* **25:** 465-498.
Bruijnzeel, L. A. and Proctor, J. 1995. Hydrology and biogeochemistry of tropical montane cloud forests: what do we really know? *Tropical Montane Cloud Forests*. L. S. Hamilton, J. O. Juvik and F. N. Scatena (eds). Springer Verlag, New York, NY, US**:** 38-78.
Bruijnzeel, L. A. and Scatena, F. N. 2011. Hydrometeorology of tropical montane cloud forests: preface. *Hydrological Processes* **25:** 319-326.
Bruijnzeel, L. A. and Veneklaas, E. J. 1998. Climatic conditions and tropical montane forest productivity: the fog has not lifted yet. *Ecology* **79 (1):** 3-9.
Brum, M., Teodoro, G. S., Abrahão, A., Oliveira, R. S. 2017. Coordination of rooting depth and leaf hydraulic traits defines drought-related strategies in the campos rupestres, a tropical montane biodiversity hotspot. *Plant Soil*, DOI 10.1007/s11104-017-3330-x.
Bubb, P., May, I. A., Miles, L. and Sayer, J. (2004). Cloud Forest Agenda. Cambridge, UK, UNEP World Conservation Monitoring Centre.
Bücker, A., Crespo, P., Frede, H. G. and Breuer, L. 2011. Solute behaviour and export rates in neotropical montane catchments under different land-uses. *Journal of Tropical Ecology* **27 (3):** 305-317.
Bücker, A., Crespo, P., Frede, H. G., K., V., Cisneros, F. and Breuer, L. 2010. Identifying controls on water chemistry of tropical cloud forest catchments: combining descriptive approaches and multivariate analysis. . *Aquatic geochemistry* **16 (1):** 127-149.
Bush, M. B., Alfonso-Reynolds, A. M., Urrego, D. H., Valencia, B. G., Correa-Metrio, Y.A., Zimmermann, M., Silman, M. R. 2015. Fire and climate: contrasting pressures on tropical Andean timberline species. *Journal of Biogeography* **42 (5):** 938-950.
Buytaert, W., Cuesta-Camacho, F. and Tobon, C. 2011. Potential impacts of climate change on the environmental services of humid tropical alpine regions. *Global Ecology and Biogeography* **20 (1):** 19-33.
Buytaert, W., Deckers, J. and Wyseure, G. 2005a. Clay mineralogy of the soils in the south Ecuadorian paramo region. *Geoderma* **127 (1-2):** 114-129.
Buytaert, W., Wyseure, G., De Bièvre, B. and Deckers, J. 2005b. The effect of land-use changes on the hydrological behaviour of Histic Andosols in south Ecuador. *Hydrological Processes* **19 (20):** 3985-3997.Buytaert, W., Deckers, J. and Wyseure, G. 2006. Description and classification of nonallophanic Andosols in south Ecuadorian alpine grasslands (páramo). *Geomorphology* **73 (3-4):** 207-221.
Buytaert, W., Iñiguez, V. and Bièvre, B. 2007. The effects of afforestation and cultivation on water yield in the Andean páramo. *Forest Ecology and Management* **251 (1-2):** 22-30.
Buytaert, W., Sevnik, J. and Cuesta, F. (2014). Cambio climático: la nueva amenaza para los páramos. Avances En Investigación Para La Conservación de Los Páramos Andinos. F. Cuesta,

J. Sevink, L. Llambí, B. De Bièvre and J. Posner. Lima,Peru, CONDESAN**:** 502-526.
Cavaleri, M.A., Ostertag, R., Cordell, S., Sack, L. 2014. Native trees show conservative water use relative to invasive trees: results from a removal experiment in a Hawaiian wet forest. *Conservation Physiology* **2(1):** cou016.
Castro, S.A.B., Silveira, F.A.O., Marcato, M.S., Lemos-Filho, J.P. 2017. So close, yet so different: Divergences in resource use may help stabilize coexistence of phylogenetically-related species in a megadiverse grassland. *Flora, in press*. DOI: 10.1016/j.flora.2016.11.018
Célleri, R. and Feyen, J. 2008. The hydrology of tropical Andean ecosystems: importance, knowledge status, and perspectives. *Mountain Research and Development* **29 (4):** 350-355.
Cernusak, L.A., Aranda, J., Marshall, J.D., Winter, K. (2007) Large variation in whole-plant water- use efficiency among tropical tree species. *New Phytologist* **173:** 294-305.
Clark, D. B., Hurtado, J. and Saatchi, S. S. 2015. Tropical Rain Forest Structure, Tree Growth and Dynamics along a 2700-m Elevational Transect in Costa Rica. *Plos One* **10 (4):** 1-18.
Clark, K.E., Torres, M.A., West, A.J., Hilton, R.G., New, M., Horwath, A.B., Fisher, J.B., Rapp, J.M., Robles Caceres, A., Malhi, Y. 2014. The hydrological regime of a forested tropical Andean catchment. *Hydrology and Earth System Sciences* **18:** 5377-5397.
Cleef, A. M., Rangel-Churio, O. and Salamanca-Villegas, S. 1983. Reconocimiento de la vegetación de la parte alta del transecto Parque Los Nevados. *La Cordillera Central Colombiana Transecto Parque Los Nevados*. T. Van der Hammen and A. P.-E. Pérez-Preciado, P. (eds). J. Cramer, Vaduz, Liechtenstein**:** 150-173.
Coltorti, M. and Ollier, C. D. 2000. Geomorphic and tectonic evolution of the Ecuadorian Andes. *Geomorphology* **32:** 1-19.
Damour, G., Simonneau, T., Cochard, H., Urban, L. 2010. An overview of models of stomatal conductance at the leaf level. *Plant Cell and Environment* **33:**1419–38.
Dias, H. F., Grosjean, M. and Graumlich, L. 2003. Climate variability and change in high elevation regions: past, present and future. *Climatic Change* **59:** 1-4.
Diaz, A., Péfaur, J.E., Durant, P. 1997. Ecology of South American Páramos with emphasis on the fauna of the Venezuelan Páramos. *Ecosystems of the world 3 - Polar and Alpine Tundra*. Wiegolaski, F.E. (ed). Elsevier, Amsterdam: 263-310.
Eller, C. B., Burgess, S. S. O. and Oliveira, R. S. 2015. Environmental controls in the water use patterns of a tropical cloud forest tree species, Drimys brasiliensis (Winteraceae). *Tree Physiology* **35:** 387-399.
Eller, C. B., Lima, A. L. and Oliveira, R. S. 2013. Foliar uptake of fog water and transport belowground alleviates drought effects in the cloud forest tree species, Drimys brasiliensis (Winteraceae). *New Phytologist* **199:** 151-162.
Eller, C. B., Lima, A. L. and Oliveira, R. S. 2016. Cloud forest trees with higher foliar water uptake capacity and anisohydric behavior are more vulnerable to drought and climate change. *New Phytologist* **211 (2):** 489-501.
Fernandes, G. W., Barbosa, N. P. U., Negreiros, D. and Paglia, A. P. 2014. Challenges for the conservation of vanishing megadiverse rupestrian grasslands. *Natureza e Conservação* **12:** 162-165.
Fleischbein, K., Wilcke, W., Goller, R., Boy, J., Valarezo, C., Zech, W., Knoblich, K. 2005. Rainfall interception in a lower montane forest in Ecuador: effects of canopy properties. *Hydrological Processes* **19:** 1355-1371.
Foster, P. N. 2001. The potential negative impacts of global climate change on tropical montane

cloud forests. *Earth-Science Reviews* **55 (1-2):** 73-106.
Frantzen, N. M. L. H. F. and Bouman, F. 1989. Dispersal and growth form patterns of some zonal paramo vegetation types. *Acta Botanica Neerlandica* **38 (4):** 449-465.
Gaff, D. F. and Oliver, M. 2013. The evolution of desiccation tolerance in angiosperm plants: a rare yet common phenomenon. *Functional Plant Biology* **40:** 315-328.
García-Coll, I. 2002. Potencial de recarga de acuíferos y estabilización de ciclos hídricos de areas forestadas. Reporte de Investigación. México: INE-DGIPEA.
Garreaud, R. D. 2009. The Andes climate and weather. Advances in Geoscience 22: 3–11.
Gerald, G., Schawe, M. and Bach, K. 2008. Hydrometeorologic, Pedologic and Vegetation Patterns along an Elevational Transect in the Montane Forest of the Bolivian Yungas. *Erde* **139 (1-2):** 141-168.
Gerald, G. 2008. Soil, climate and vegetation of tropical montane forests – a case study from the Yungas, Bolivia. In: S. Robbert Gradstein, Jürgen Homeier and Dirk Gansert (Eds.) *The Tropical Mountain Forest*, *Patterns and Processes in a Biodiversity Hotspot* .Göttingen Centre for Biodiversity and Ecology- Biodiversity and Ecology Series, Vol. 2, cap. 9, 10, German, 2008, pag. 137-162.
Gibbs, H. K., Ruesch, A. S., Achard, F., Clayton, M. K., Holmgrem, P., Ramankutty, N. and Foley, J. A. 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Science* **107 (38):** 16732-16737.
Girardin, C.A.J. *et al.* 2014. Spatial patterns of above-ground structure, biomass and composition in a network of six Andean elevation transects. *Plant Ecology & Diversity* **7(1-2):** 161-171.
Giulietti, A.M., Menezes, N.L., Pirani, J.R., Meguro, M., Wanderley, M.G. 1987. Flora da Serra do Cipó, Minas Gerais: caracterização das espécies. *Boletim de Botânica da Universidade de São Paulo* **9:** 1-152
Goldsmith, G. R., Bentley, L. P., Shenkin, A., Salinas, N., Blonder, B., Martin, R. E., Castro-Ccossco, R., Chambi-Porroa, P., Diaz, S., Enquist, B. J., Asner, G. P. and Malhi, Y. 2016. Variation in leaf wettability traits along a tropical montane elvation gradient. *New Phytologist***:** 1-14.
Goldsmith, G. R., Matzke, N. J. and Dawson, T. E. 2013. The incidence and implications of clouds for cloud forest plant water relations. *Ecology Letters* **16:** 307-314.
Good, S.P., Moore, G.W., Miralles, D.G. 2017. A mesic maximum in biological water use demarcates biome sensitivity to aridity shifts. *Nature Ecology & Evolution*: 10.1038/s41559-017-0371-8.
Gotsch, S.G., Asbjornsen, H., Holwerda, F., Goldsmith, G.R., Weintraub, A.E., Dawson, T.E. 2014. Foggy days and dry nights determine crown-level water balance in a seasonal tropical montane cloud forest. *Plant, Cell and Environment* **37:** 261-272.
Gotsch, S. G., Nadkarni, N., Darby, A., Glunk, A., Dix, M., Davidson, K. and Dawson, T. E. 2015. Life in the treetops: ecophysiological strategies of canopy epiphytes in a tropical montane cloud forest. *Ecological Monographs* **85 (3):** 393-412.
Gotsch, S.G., Asbjornsen, H., Goldsmith, G.R. 2016. Plant carbon and water fluxes in tropical montane cloud forests. *Journal of Tropical Ecology* **32(5):** 404-420.
Graefe, S., Hertel, D. and Leuschner, C. 2008. Estimating fine root turnover in tropical forests along an elevational transect using minirhizotrons. *Biotropica* **40 (5):** 536-542.
Graefe, S., Hertel, D. and Leuschner, C. 2010. N, P and K limitation of fine root growth along an elevation transect in tropical mountain forests. *Acta Oecologica* **36 (6):** 537-542.

Grubb, P. J. 1974. Factors controlling the distribution of forests types on tropical mountains: new facts and a new perspective. *Altitudinal Zonation in Malesia*. J. R. Flenley (eds). University of Hull Geography Department, Hull, England**:** 1-25.
Grubb, P. J. 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. *Annual Review of Ecological Systems* **8:** 83-107.
Grubb, P. J. and Whitmore, T. C. 1966. A lowland comparison of montane and lowland rain forest in Ecuador II: the climate and its effects on the distribution and physiognomy of the forests. *Journal of ecology* **54:** 303-333.
Hafkenscheid, R. L. L. J. (2000). Hydrology and biogeochemistry of montane rain forests of contrasting stature in the Blue Mountains of Jamaica. PhD, Vrije Universiteit.
Hager, A., Dohrenbusch, A. 2011. Hydrometeorology and structure of tropical montane cloud forests under contrasting biophysical conditions in north-western Costa Rica. *Hydrological Processes* **25:** 392-401.

Hamilton, L. S., Juvik, J. O. and Scatena, F. N. 1995. The Puerto Rico Tropical Cloud Forest Symposium: Introduction and Workshop Synthesis. *Tropical Montane Cloud Forests: Proceedings of an International Symposium*. L. S. Hamilton, J. O. Juvik and F. N. Scatena (eds). Springer Verlag, New York, NY, US**:** 150-155.
Hensen, I., A. Cierjacks, H. Hirsch, M. Kessler, K. Romoleroux, D. Renison, K. Wesche. 2012. Historic and recent fragmentation coupled with altitude affect the genetic population structure of one of the world's highest tropical tree line species. *Global Ecology and Biogeography* **21(4)**: 455–464.
Hernandez, L., Dezzeo, N., Sanoja, E., Salazar, L., Castellanos, H. 2012. Changes in structure and composition of evergreen forests on an altitudinal gradient in the Venezuelan Guayana shield. *Revista de Biologia Tropical* **60:** 11-33
Hietz, P. 2010. Ecology and ecophysiology of epiphytes in tropical montane cloud forests. *Tropical Montane Cloud Forests: Science for Conservation and Management*. L. A. Bruijnzeel, F. N. Scatena and L. S. Hamilton (eds). Cambridge University Press, Cambridge, UK**:** 739.
Holder, C. D. 2007. Leaf water repellency as an adaptation to tropical montane cloud forest environments. *Biotropica* **39 (6):** 767-770.
Holdridge, L. R. 1967. *Life Zone Ecology, Rev. Ed. With Photographic Supplement Prepared by J. A. Tosi, Jr.* TROPICAL SCIENCE CENTER: San Jose, Costa Rica.
Holscher, D., Kohler, L., van Dijk, A. I. J. M., Bruijnzeel, L. A. 2004. The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. *Journal of Hydrology* **292:** 308-322.
Homeier, J., Breckle, S.-W., Gunter, S., Rollenbeck, R. T. and Leuschner, C. 2010. Tree Diversity, Forest Structure and Productivity along Altitudinal and Topographical Gradients in a Species Rich Ecuadorian Montane Rain Forest. *Biotropica* **42 (2):** 140-148.
Holwerda, F., L.A. Bruijnzeel, L.E. Muñoz-Villers, Gomez-Cardenas, M. M. Equihua, H. Asbjornsen. 2010. Rainfall and cloud water interception in mature and secondary lower montane cloud forests of central Veracruz, Mexico. Hydrological Processes. *Journal of Hydrology* **384:** 84–96.
IPCC. 2014. *Climate Change 2007: Impacts, Adaptation, and Vulnerability - Part B: Regional Aspects*. University of Cambridge, New York, NY, USA, 696.
IUFRO.2000. Forests in sustainable mountain development: a state of knowledge report for

2000. IUFRO Research Series. M. F. Price and N. Butt. London, UK, IUFRO. **5:** 591.
Jacobi, C. M., Carmo, F. F., Vincent, R. C. and Stehmann, J. R. 2007. Plant communities on ironstone outcrops: a diverse and endangered Brazilian ecosystem. *Biodiversity and Conservation* **16:** 2185-2200.
Jarvis, A. and Mulligan, M. 2011. The climate of tropical montane cloud forests. *Hydrological Processes* **25:** 327-343.
Jasechko, S., Sharp, Z. D., Gibson, J. J., Birks, S. J., Yi, Y. and Fawcett, P. J. 2013. Terrestrial water fluxes dominated by transpiration. *Nature* **496:** 347-351.
Jørgensen, P. M., Ulloa-Ulloa, C., León, B., León, Y., Beck, S. G., Nee, M., Zarucchi, J. L., Celis, M. and Bernal, R. G. R. 2011. Regional Patterns of Vascular Plant Diversity and Endemism. *Climate Change and Biodiversity in the Tropical Andes*. S. K. Herzog, R. Martínez, P. M. Jørgensen and M. Tiessen (eds). Inter–American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), Inter–American Institute for Global Change Research (IAI).
Jimenez-Castillo, M., Lusk, C.H. 2013. Vascular performance of woody plants in a temperate rain forest: lianas suffer higher levels of freeze–thaw embolism than associated trees. *Functional Ecology*, **27**: 403-412.
Kessler, M. 2001. Patterns of diversity and range size of selected groups along an elevational transect in the Bolivian Andes. *Biodiversity and Conservation* **10:** 1897-1921.
Kleier, C.C. 2001. Functional ecology, ecophysiology, and convergent evolution of dwarf shrub and cushion plant forms. PhD Thesis. University of California, Los Angeles, USA, 180 pp.
Kohler, L., Tobon, C., Frumau, K.F.A., Bruijnzeel, L.A. 2007. Biomass and water storage dynamics of epiphytes in old-growth and secondary montane cloud forest stands in Costa Rica. *Plant Ecology*, **193:** 171-184.
Lambrinos, J.G., Kleier, C.C., Rundel, P.W. 2006. Plant community variation across a puna landscape in the Chilean Andes. *Revista Chilena de Historia Natural* **79:** 233-243.
Lawton, R. O. 1984. Ecological constraints on wood density in a tropical montane rain forest. *American Journal of Botany* **71:** 261-267.
Leon, J.D.; Osorio, N.W. 2014. Role of litter turnover in soil quality in tropical degraded lands of Colombia. *Scientific World Journal*: 1-11.
Le Stradic, S., Buisson, E. and Fernandes, G. W. 2015. Vegetation composition and structure of some Neotropical mountaind grasslands in Brazil. *Journal of Mountain Science* **12:** 864-877.
Letts, M. G., Mulligan, M., Rincon-Romero, M. E. and Bruijnzeel, L. A. 2010. Environmental controls on photosynthetic rates of lower montane cloud forest vegetation in south-western Colombia. *Tropical montane cloud forests: science for conservation and management*. L. A. Bruijnzeel, F. N. Scatena and L. S. Hamilton (eds). Cambridge University Press, New York**:** 768.
Leuschner, C., Moser, G., Bertsch, C., Röderstein, M. and Hertel, D. 2007. Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. *Basic and Applied Ecology* **8 (3):** 219-230.
Lieberman, D., Lieberman, M., Peralta, R. and Hartshorn, G. S. 1996. Tropical forest structure and composition on a large- scale altitudinal gradient in Costa Rica. *Journal of ecology* **84:** 137-152.
Longhi, S. J., Brena, D. A., Ribeiro, S. B., Gracioli, C. R., Longhi, R. V. and Mastella, T. 2009. Ecological factors that determine the occurrence of Araucaria angustifolia and Podocarpus lambertii in Mixed Ombrophylous Forest at São Francisco de Paula's FLONA, RS, Brazil.

Ciencia Rural **40(1):** Online **-** ISSN 1678-4596.
Luteyn, J. L. 1992. Páramos: why study them? *Páramo: An Andean Ecosystem Under Human Influence*. H. Balsley and J. L. Luteyn (eds). Academic Press, London, UK**:** 1-14.
Luteyn, J. L. 1999. *Páramos: A checklist of plant diversity, geographic distribution, and botanical literature*. The New York Botanical Garden Press: New York, NY, USA;
Luteyn, J. L. 2005. Introducción al ecosistema de páramo. *Páramos de Costa Rica*. M. Kappelle and S. Horn (eds). Editorial INBio, Santo Domingo de Heredia, Costa Rica**:** 37-99.
Madriñán, S., Cortés, A. J. and Richardson, J. E. 2013. Páramo is the world's fastest evolving and coolest biodiversity hotspot. *Frontiers in Genetics* **4:** 1-7.
Malhado, A. C. M., Malhi, Y., Whittaker, R. J., Ladle, R. J., Ter Steege, H., Fabre, N. N., Phillips, O., Laurance, W. F., Aragao, L. E. O. C. and Pitman, N. C. A. 2012. Drip-tips are associated with intensity of precipitation in the Amazon rain forest. *Biotropica* **44:** 728-737.
Malhi, Y. and Wright, J. 2004. Spatial patterns and recent trends in the climate of tropical rainforest regions. *The Royal Society* **359:** 311-329.
Martin, P.H., Fahey, T.J., Sherman, R.E. 2010. Vegetation zonation in a Neotropical montane forest: environment, disturbance and ecotones. *Biotropica* **43(5):** 533-543.
Martínez, R., Ruiz, D., Andrade, M., Blacutt, L., Pabón, D., Jaimes, E., León, G., Villacís, M., Quintana, J. and Montealegre, E. 2011. Synthesis of the climate of the tropical Andes. *Climate Change and Biodiversity in the Tropical Andes*. S. K. Herzog, R. Martínez and P. M. T. Jørgensen, M. (eds). Inter–American Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), Inter-American Institute of Global Change Research (IAI)**:** 97-109.
McDowell, N.G., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Willians, D.G., Yepez, E.A. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* **178:**719–739.
Monasterio, M. and Sarmiento, G. 1991. Adaptive radiation of Espeletia in the cold Andean tropics. *Trends in Ecology and Evolution* **6:** 387-391.
Moore, P. D. 2008. *Tropical Forests*. Facts on File, Inc.: New York, NY; pp.245.
Mosquera, G. M., Lazo, P. X., Celleri, R., Wilcox, B. P. and Crespo, P. 2015. Runoff from tropical alpine grasslands increases with areal extent of wetlands. *Catena* **125:** 120-128.
Mosquera, G. M., Celleri, R., Lazo, P. X., Vaché, K., Perakis, S. S. and Crespo, P. 2016a. Combined Use of Isotopic and Hydrometric Data to Conceptualize Ecohydrological Processes in a High-Elevation Tropical Ecosystem. *Hydrological Processes* **30 (17):** 2930-2947.
Mosquera, G. M., Segura, C., Vaché, K., Windhorst, D., Breuer, L. and Crespo, P. 2016b. Insights on the water mean transit time in a high-elevation tropical ecosystem. *Hydrology and Eart System Sciences Discussions* **20:** 2987-3004.
Motzer, T., Munz, N., Kuppers, M., Schmitt, D. and Anhuf, D. 2005. Stomatal conductance, transpiration and sap flow of tropical montane rain forest trees in the southern Ecuadorian Andes. *Tree Physiology* **25:** 1283-1293.
Mulligan, M. 2010. Modeling the tropics-wide extent and distribution of cloud forest and cloud forest loss, with implications for conservation priority. *Tropical Montane Cloud Forests: Science for Conservation and Management*. L. A. Bruijnzeel, F. N. Scatena and L. S. Hamilton (eds). Cambridge University Press, Cambridge, UK**:** 14-38.
Muñoz-Villers, L.E., Holwerda, F., Gomez-Cardenas, M., Equihua, M., Asbjornsen, H.,

Bruijnzeel, L.A., Marin-Castro, B.E., Tobon, C. 2012. Water balances of old-growth and regenerating montane cloud forests in central Veracruz, Mexico. *Journal of Hydrology* **462-463:** 53-66.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403** (6772): 853–858.

Nicholson, S. E. 2011. *Dryland Climatology*. Cambridge University Press: Cambridge, UK;

Nogués-Bravo, D., Araújo, M. B., Errea, M. P. and Martínez-Rica, J. P. 2007. Exposure of global mountain systems to climate warming during the 21st century. *Global Environmental Change* **17:** 420-428.

Oliveira, R. S., Dawson, T. E. and Burgess, S. S. O. 2005. Evidence for direct water absorption by the shoot of the desiccation-tolerant plant Vellozia flavicans in the savannas of central Brazil. *Journal of Tropical Ecology* **21 (5):** 585-588.Oliveira, R. S., Abrahão, A., Pereira, C., Teodoro, G. S., Brum, M., Alcantara, S. and Lambers, H. 2016. Ecophysiology of Campos Rupestres Plants. *Ecology and Conservation of Mountaintop Grasslands in Brazil*. G. W. Fernandes (eds). Springer International Publishing, New York, NY, US**:** 567.

Oliveira, R.S., Christoffersen, B.O., Barros, F.V., Teodoro, G.S., Bittencourt, P., Brum, M.M., Viani, R.A.G. 2014a. Changing precipitation regimes and the water and carbon economies of trees. *Theoretical and Experimental Plant Physiology* **26:** 65-82.

Oliveira, R. S., Eller, C. B., Bittencourt, P. R. L. and Mulligan, M. 2014b. The hydroclimatic and ecophysiological basis of cloud forest distributions under current and projected climates. *Annals of Botany* **113 (6):** 909-920.

Oliveira, R. S., Galvão, H. C., Campos, M. C. R., Eller, C. B., Pearse, S. J. and H., L. 2015. Mineral nutrition of campos rupestres plant species on contrasting nutrient-impoverished soil types. *New Phytologist* **205 (3):** 1183-1194.

Oliveira, V., Costa, A. M. R., Azevedo, W. P., Camargo, M. N. and Larach, J. O. I. 1983. Pedologia. Projeto Radam-Brasil. Rio de Janeiro, RJ, Brazil, Ministerio das Minas e Energia. **Levantamento de Recursos Naturais (Rio de Janeiro/Vitoria):** 23-24.

Padrón, R. S., Wilcox, B. P., Crespo, P., Célleri, R. 2015. Rainfall in the Andean Páramo: New Insights from High-Resolution Monitoring in Southern Ecuador. *Journal of Hydrometeorology* **16 (3):** 985-996.

Oliveras et al. 2013. Changes in forest structure and composition after fire in tropical montane cloud forests near the Andean treeline. *Plant Ecology & Diversity* **7(1-2):** 329-340.

Pepin *et al.* 2015. Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*. **5**: 424-430.

Perez, C. A., Frangi, J. L. 2000. Grassland biomass dynamics along an altitudinal gradient in the Pampa. *Journal of Range Management* **53:** 518-528.

Pielke, R.A., Adegoke, J., Beltrán-Przekurat, C.A., Hiemstra, C.A., Lin, J., Nair, U.S., Niyogi, D., Nobis, T.E. 2007. An overview of regional land-use and land-cover impacts on rainfall. *Tellus* **59(3):** 587-601.

Pinto, L. C., Mello, C. R., Owens, P. R., Norton, L. D. , Curi, N. 2015. Role of Inceptisols in the Hydrology of Mountainous Catchments in Southeastern Brazil. *Journal of Hydrologic Engineering* **21 (2):** 1-10.

Podwojewski, P., Poulenard, J., Zambrana, T., Hofstede, R. 2002. Overgrazing effects on vegetation cover and properties of volcanic ash soil in the páramo of Llangahua and La Esperanza (Tungurahua, Ecuador). *Soil Use and Management* **18 (1):** 45-55.

Ponce-Reyes, R., Reynoso-Rosales,V.-H., Watson, J.E.M., Van der Wal, J., Fuller, R.A., Pressey, R.L., Possingham, H.P. 2012. Vulnerability of cloud forest reserves in Mexico to climate change. *Nature Climate Change* **2:**448–452.

Ponette-Gonzalez, A. G., Weathers, K. C. and Curran, L. M. 2009. Water inputs across a tropical montane landscape in Veracruz, Mexico: synergistic effects of land cover, rain and fog seasonality, and interannual precipitation variability. *Global Change Biology* **16 (3):** 946-963.Porembski, S. and Barthlott, W. 2000. Granitic and gneissic outcrops (inselbergs) as centers of diversity for desiccation-tolerant vascular plants. *Plant Ecology* **151:** 19-28.

Poulenard, J., Michel, J. C., Bartoli, F., Portal, J. M. and Podwojewski, P. 2004. Water repellency of volcanic ash soils from Ecuadorian páramo: effect of water content and characteristics of hydrophobic organic matter. *European Journal of Soil Science* **55 (3):** 487-496.

Poulenard, J., Podwojewski, P. and Herbillon, A. J. 2003. Characteristics of non-allophanic Andisols with hydric properties from the Ecuadorian páramos. *Geoderma* **117 (3):** 267-281.

Poulenard, J., Podwojewski, P., Janeau, J.-L. and Collinet, J. 2001. Runoff and soil erosion under rainfall simulation of Andisols from the Ecuadorian Páramo: effect of tillage and burning. *Catena* **45 (3):** 185-207.

Prada, C.M., Stevenson, P.R. 2016. Plant composition associated with environmental gradients in tropical montane forests (Cueva de Los Guacharos National Park, Huila, Colombia). *Biotropica* **48(5):** 568-576.

Ramsay, P. M., Oxley, E. R. B. 1997. The growth form composition of plant communities in the ecuadorian páramos. *Plant Ecology* **131 (2):** 173-192.

Reis, M. S., Ladio, A. and Peroni, N. 2014. Landscapes with Araucaria in South America: evidence for a cultural dimension. *Ecology and Society* **19 (2):** 43-57.

Restrepo et al. 2009. Landsliding and its multiscale influence on mountainscapes. Bioscience, **59(8):** 685-698.

Richter, M. 2008. Tropical mountain forests - distribution and general features. *The tropical mountain forest: Patterns and Processes in a biodiversity hotspot*. S. R. Gradstein, J. Homeier and D. Gansert (eds). Göttigen Centre for Biodiversity and Ecology, Göttigen, Germany. **2:** 224.

Rollenbeck, R., J. Bendix, P. Fabian. 2011. Spatial and temporal dynamics of atmospheric water inputs in tropical mountain forests of South Ecuador. *Hydrological Processes* **25(3):** 344–352.

Rosado, B. H. P., Oliveira, R. S. and Aidar, M. P. M. 2010. Is leaf water repellency related to vapor pressure deficit and crown exposure in tropical forests? *Acta Oecologica* **36:** 645-649.

Safford, H. D. 1999. Brazilian Paramos IV: An introduction to the physical environment and vegetation of the campos de altitude. *Journal of Biogeography* **26:** 693-712.

Safford, H. D. 2007. Brazilian Paramos IV: Phytogeography of the campos de altitude. *Journal of Biogeography* **34:** 1701-1722.

Sanchez, M., Pedroni, F., Eisenlohr, P.V., Oliveira-Filho, A.T. 2013. Changes in tree community composition and structure of Atlantic rain forest on a slope of the Serra do Mar range, southeastern Brazil, from near sea level to 1000 m of altitude. *Flora* **208(3):** 184-196.

Sarmiento, G. 1986. Ecologically crucial features of climate in high tropical mountains. *High Altitude Tropical Biogeography*. F. Vuilleumier and M. Monasterio (eds). Oxford University Press, Oxford, UK**:** 11-45.

Scarano, F. R. 2002. Structure, Function and Floristic Relationships of Plant Communities in Stressful Habitats Marginal to the Brazilian Atlantic Rainforest. *Annals of Botany* **90:** 517-524.

Scarano, F. R. 2009. Plant communities at the periphery of the Atlantic rain forest: Rare-species

bias and its risks for conservation. *Biological Conservation* **142:** 693-712.
Schwalm, C.R. *et al.* 2017. Global patterns of drought recovery. *Nature* **548:** 202-205
Schubert, C. 1980. Contribution de Venezuela al inventatio mundial de glaciares. *Boletin de Ciencias Naturales* **34 (137):** 267-279.
Schuldt, B., Leuschner, C., Horna, V., Moser, G., Köhler, M., van Straaten, O., Barus, H. 2011. Change in hydraulic properties and leaf traits in a tall rainforest tree species subject to long-term throughfall exclusion in the perhumid tropics. *Biogeosciences* **8:** 2179-2194.
Sherman, R.E., Martin, P.H., Fahey, T.J., Degloria, S.D. 2008. Fire and vegetation dynamics in high-elevation neotropical montane forests of the Dominican Republic. *Ambio* **37(7-8)**: 535-541.
Silveira, F. A. O., Negreiros, D., Barbosa, N. P. U., Buisson, E., Carmo, F. F., Carstensen, D. W., Conceição, A. A., Cornelissen, T. G., Echternacht, L., Fernandes, G. W., Garcia, Q. S., Guerra, T. J., Jacobi, C. M., Lemos-Filho, J. P., Le Stradic, S., Morellato, L. P., Neves, F. S., Oliveira, R. S., Schaefer, C. E., Viana, P. L. and Lambers, H. 2016. Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. *Plant and Soil* **403 (1):** 129-152.
Sklenar, P. and Jorgensen, P. M. 1999. Distribution patterns of paramo plants in Ecuador. *Journal of Biogeography* **26 (4):** 681-691.
Soares, P. V., Pereira, S. Y., Simoes, S. J. C., Bernardes, G. P., Barbosa, S. A. and Trannin, I. C. B. 2012. The definition of potential infiltration areas in Guaratinguetá watershed, Paraíba do Sul Basin, Southeastern Brazil: an integrated approach using physical and land-use elements. *Environmental and Earth Science* **67:** 1685-1694.
Soethe, N., Lehmann, J. and Engels, C. 2008. Nutrient availability at different altitudes in a tropical montane forest in Ecuador. *Journal of Tropical Ecology* **24 (4):** 397-406.
Spracklen, D. V., Righelato, R. 2014. Tropical montane forests are a larger than expected global carbon store. *Biogeosciences* **11:** 2741-2754.
Spehn, E., Liberman, M. and Korner, C. 2006. *Land use change and mountain biodiversity*. CRC Press - Taylor & Francis Group: Boca Raton, FL.
Stadtmüller, T. 1987. *Cloud forests in the humid tropics: a bibliographic review*. United Nations University, Tokyo and CATIE, Turrialba, Costa Rica: Tokyo, Japan.
Stanton, D.E., Chavez, J.H., Villegas, L., Villasante, F., Armesto, J., Hedin, L.O., Horn, H. 2014. Epiphytes improve host plant water use by microenvironment modification. *Functional Ecology*, **28:** 1274-1283.
Still, C. J., Foster, P. N. and Schneider, S. H. 1999. Simulating the effects of climate change on tropical montane cloud forests. *Nature* **398:** 608-610.
Subramaniam, A., P.L. Yager, E.J. Carpenter, C. Mahaffey, K. Bjorkman, S. Cooley. A.B. Kustka, J.P. Montoya, S.A. Sanudo-Wilhelmy, R. Shipe, D.G. Capone. 2007. Amazon River enhances diazotrophy and carbon sequestration in the tropical North Atlantic Ocean. *Proceedings of the National Academy of Sciences* **205(30):**10460-10465.
Teale, N. G., Mahan, H., Bleakney, S., Berger, A., Shibley, N., Frauenfeld, O. W., Quiring, S. M., Rapp, A. D., Roark, E. B. and Washington-Allen, R. 2014. Impacts of Vegetation and Precipitation on Throughfall Heterogeneity in a TropicalPre-Montane Transitional Cloud Forest. *Biotropica* **46 (6):** 667-676.
Thomaz, E. L. 2007. Dinâmica do uso da terra e degradação do solo na bacia do Rio Guabiroba - Guarapuava/PR. *Raega* **13:** 109-128.

Thomaz, E.L., Antoneli, V. 2015. Rain interception in a secondary fragment of araucaria forest with faxinal, Guarapuava-PR. *Cerne* **21 (3)**: 363-369.

Turner, I. M. 2004. *The ecology of tropical rain forest*. Cambridge Univeristy Press: Cambridge, United Kingdom; pp. 314.

van der Hammen, T. and Hooghiemstra, H. 2000. Neogene and quaternary history of vegetation, climate and plant diversity in Amazonia. *Quaternary Science Reviews* **19 (8):** 725-742.

Van Stan, J.T., Pypker, T.G. 2015. A review and evaluation of forest canopy epiphyte roles in the partitioning and chemical alteration of precipitation. *Science of the total environment*, **536:** 813-824.

Vazquez, J.A. and Givnish, T.J. 1998. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan. *Journal of Ecology* **86:** 999-1020.

Veneklaas, E.J., van Ek, R. 1990. Rainfall interception in two tropical montane rain forests, Colombia. *Hydrological Processes* **4:** 311-326.

Vitarelli, N.C., Riina, R., Cassino, M.F., Meira, R.M.S.A. 2016. Trichome-like emergences in Croton of Brazilian highland rock outrcrops: Evidences for atmospheric water uptake. *Perspectives in Plant Ecology, Evolution and Systematics* **22:** 23-35.

Vuille, M., Bradley, R. S. and Keimig, F. 2000. Climate Variability in the Andes of Ecuador and Its Relation to Tropical Pacific and Atlantic Sea Surface Temperature Anomalies. *Journal of Climate* **13:** 2520-2535.

Weaver, P. L., Byer, M. D. and Bruck, D. L. 1973. Transpiration Rates in the Luquillo Mountains of Puerto Rico. *Biotropica* **5 (2):** 123-133.

Wilcke, W., Oelmann, Y., Schmitt, A., Valarezo, C., Zech, W. and Homeier, J. 2008. Soil properties and tree growth along an altitudinal transect in Ecuadorian tropical montane forest. *Journal of Plant Nutrition and Soil Science* **171 (2):** 220-230.

Wilcke, W., Yasin, S., Abramowski, U., Valarezo, C. and Zech, W. 2002. Nutrient storage and turnover in organic layers under tropical montane rain forest in Ecuador. *European Journal of Soil Science* **53 (1):** 15-27.

Wilcke, W., Yasin, S., Valarezo, C. and Zech, W. 2001. Change in water quality during the passage through a tropical montane rain forest in Ecuador. *Biogeochemistry* **55 (1):** 45-72.

Wohl, E., Barros, A., Brunsell, N., Chappell, N. A., Coe, M., Giambelluca, T. W., Goldsmith, S., Harmon, R., Hendrickx, J. M. H., Juvik, J. O., Mcdonnell, J. and Ogden, F. 2012. The hydrology of the humid tropics. *Nature Climate Change* **2:** 655-662.

TABLE

Table 1. General vegetation and climate characteristics of tropical mountainous ecosystems in the Neotropics.

Vegetation type		Altitude (m.a.s.l)	Precipitation (mm year^{-1})	Seasonality (nº dry months)
Forest	Tropical Montane Rain Forest (TMRF)	700–2,500	3,000–8,000	5-6 [a]
	Tropical Montane Cloud Forest (TMCF)	800–3,500	2,000–3,500	0-3 [a]
Grassland/Scrublands	*Campo rupestre*	900–2,100	1,100–1,800	5-6 [b]
	Campo de altitude	1,800–2,900	1,500–3,000	1-3
	Páramos	3,000–4,500	700–3,000	2-5 [c]
	Punas	3,200–5,000	1,000-2,000	6-8 [b]

[a] Dry season characterized by lower precipitation rates, but rarely below 100 mm month^{-1}.
[b] In the driest months, part of these ecosystems can have no precipitation.
[c] Depending on the location, the precipitation regime may be unimodal or bimodal, but in general, yearly seasonality is low.

FIGURE LEGENDS

Figure 1. Examples of Neotropical montane ecosystems. (A–B): Transitional premontane–montane tropical rainforest in Costa Rica (San Isidro de Peñas Blancas–Texas A&M University Soltis Center) at ~600 m.a.s.l; (C–D): Tropical montane cloud forest in Brazil (RPPN Alto-Montana, Itamonte, Brazil) at 1400–2400 m.a.s.l; (E–F): Páramos grasslands in Ecuador (Zhurucay River Ecohydrological Observatory, San Fernando, Ecuador) at 3400–3900 m.a.s.l; (G–H): Campos rupestres in Brazil (Serra do Cipó National Park, Minas Gerais, Brazil) at 1200 m.a.s.l; (I–J): Campos de altitude in Brazil (Campos do Jordão National Park, Campos do Jordão, São Paulo, Brazil) above 1500 m.a.s.l.
Photo credits: A – Georgianne Moore; B – Luiza Aparecido; C & D – Patricia Pompeu; E – Giovanny Mosquera; F – Ximena Palomque; G & H – Grazielle Teodoro; I & J – Hans Lambers

Figure 2. Map of the geographic distribution of the described Neotropical montane ecosystems. These include: Tropical Montane Cloud Forest (TMCF), Tropical Montane Rain Forest (TMRF), *Páramos*, *Punas*, *Campos de altitude* and *Campos rupestres*. Dots represent research field sites referenced by geographic coordinates collected in the literature based on the montane ecosystem's classification and each Neotropical country's parks and reserves focusing on their altitude, vegetation and climatic conditions to distinguish the montane ecosystem type. The data points used and links to these references are available as supplementary material. Additionally, the full colored areas represent entire biomes delineated through polygon shapefiles - geospatial vector data format for geographic information system (GIS) – processed using R software with the maptool package (Bivand & Lewin-Koh, 2017). Shapefiles were obtained from previously published studies (Silveira *et al.*, 2015; Mulligan, 2010) and from the ArcGis site, when available (www.arcgis.com).

Figure 3. Rosettes as an example of convergence of plant life forms in Neotropical grass/scrublands: (A) *Páramos* in Ecuador – *Espeletia* sp. (Asteraceae); (B) and (C) *Campos rupestres* in Brazil – *Vellozia* sp. (Velloziaceae) and Eriocaulaceae sp. (Eriocaulaceae).
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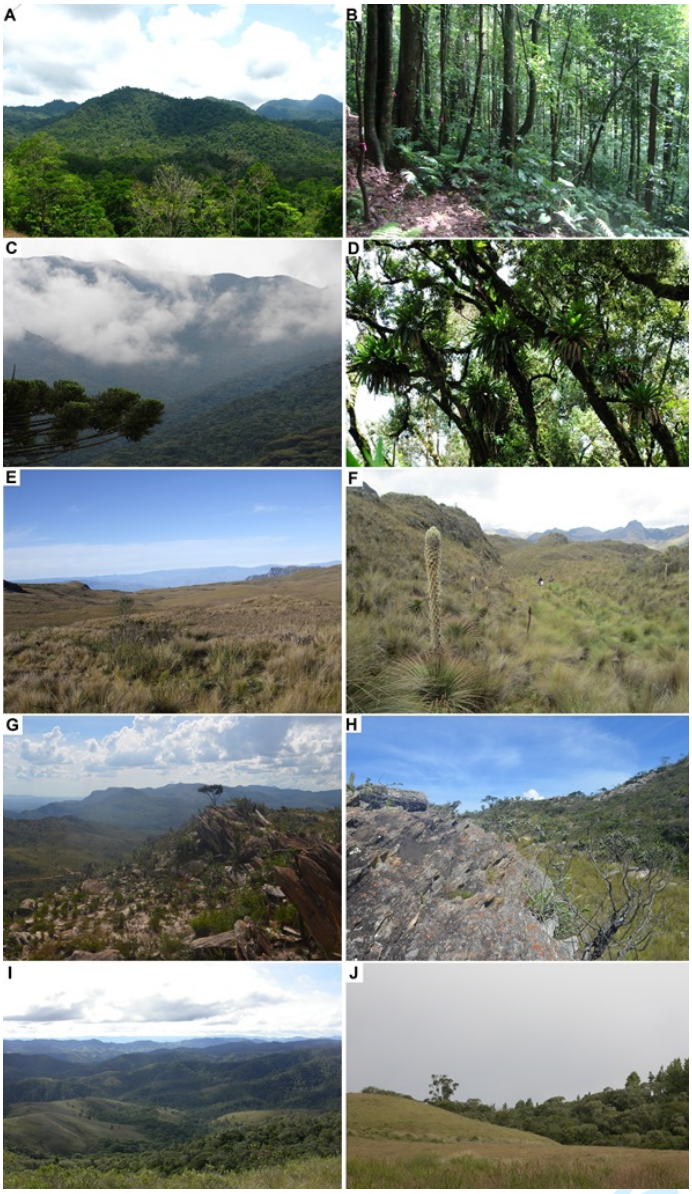
FIGURES



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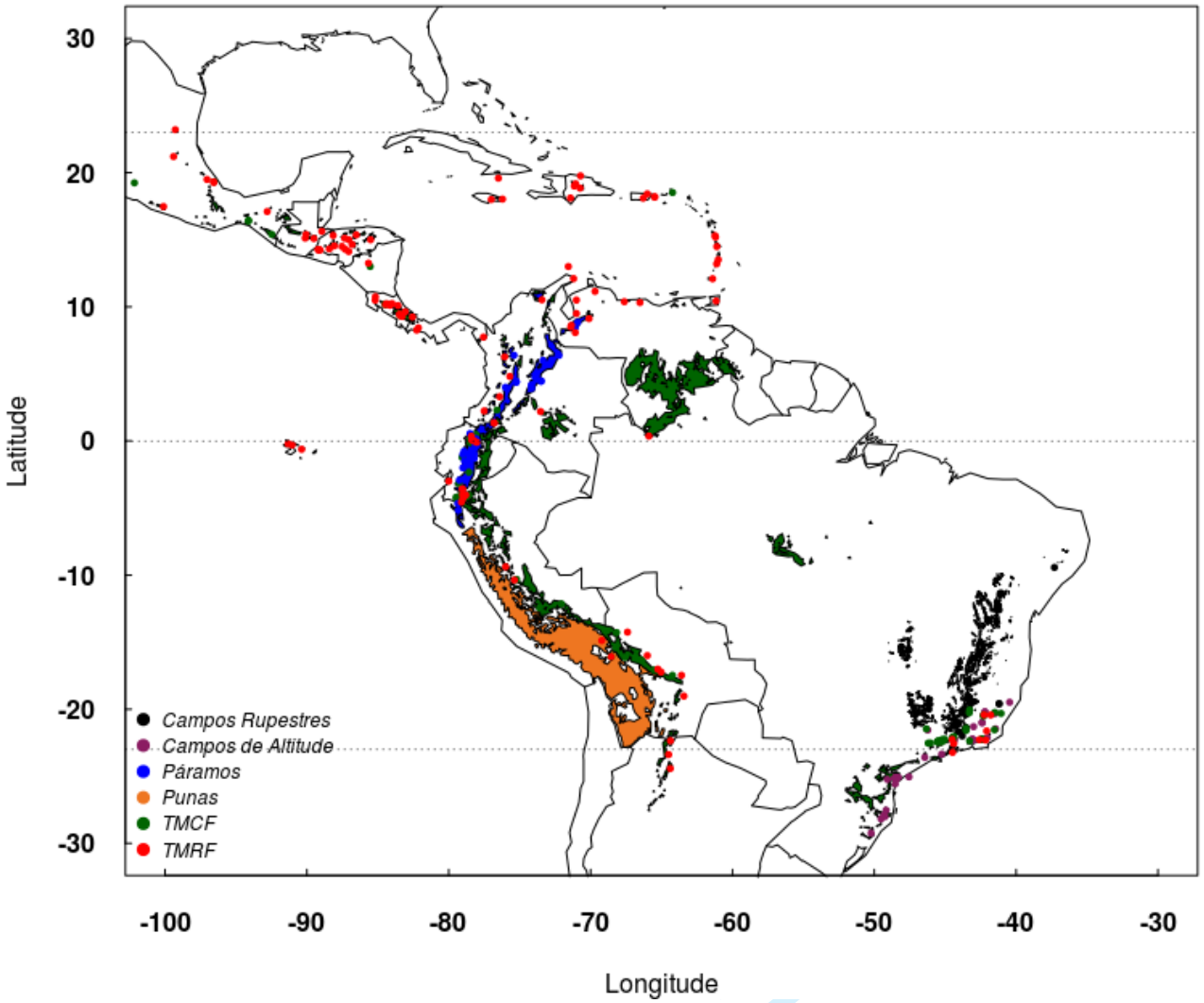

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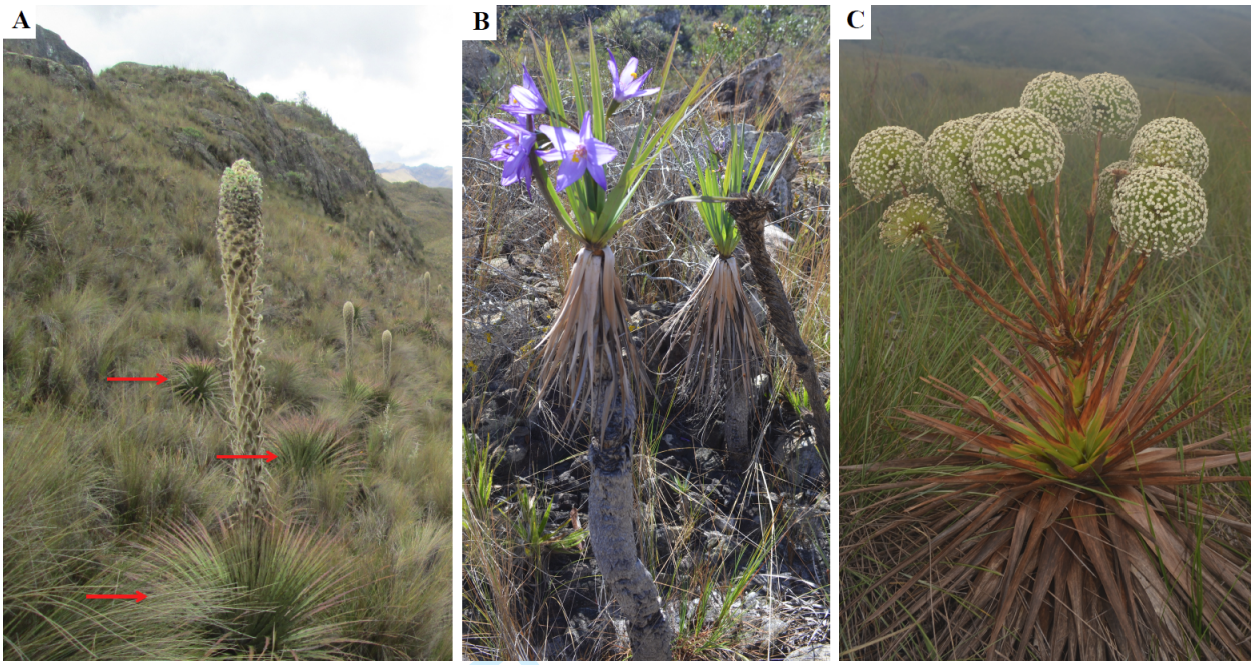

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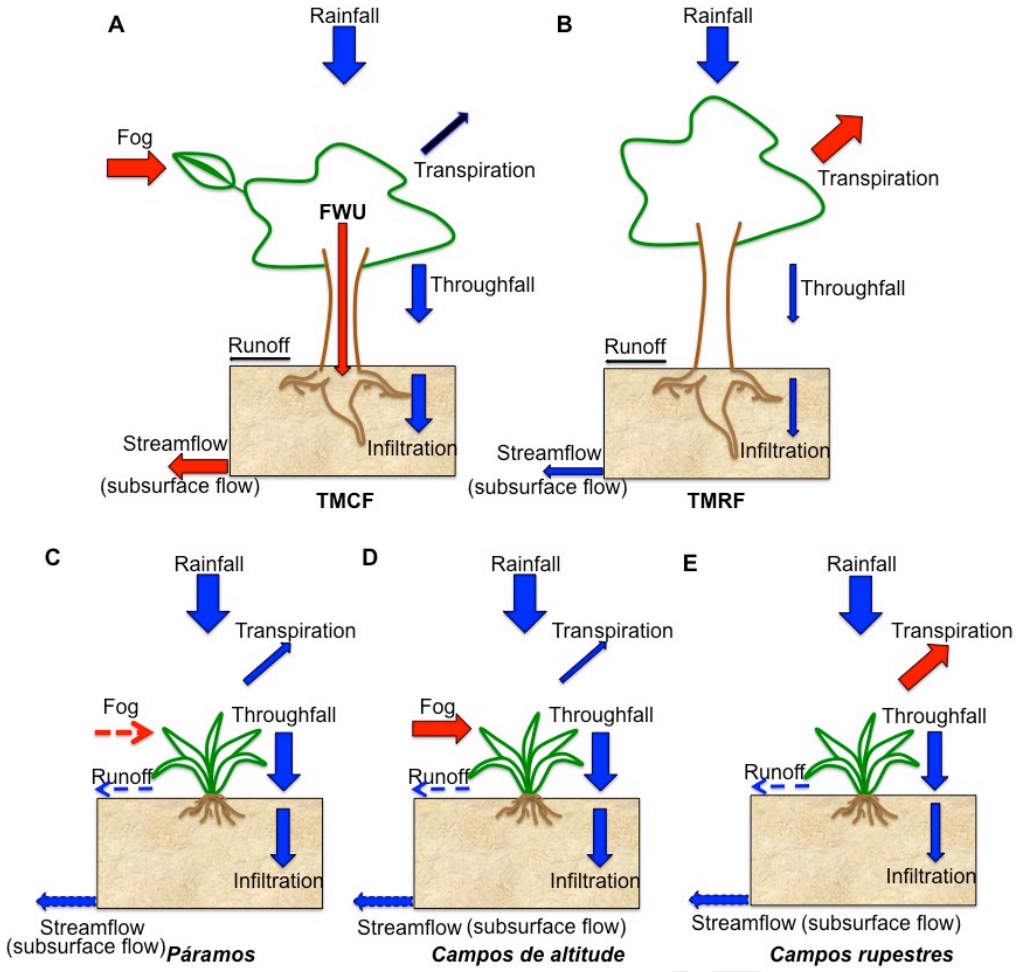

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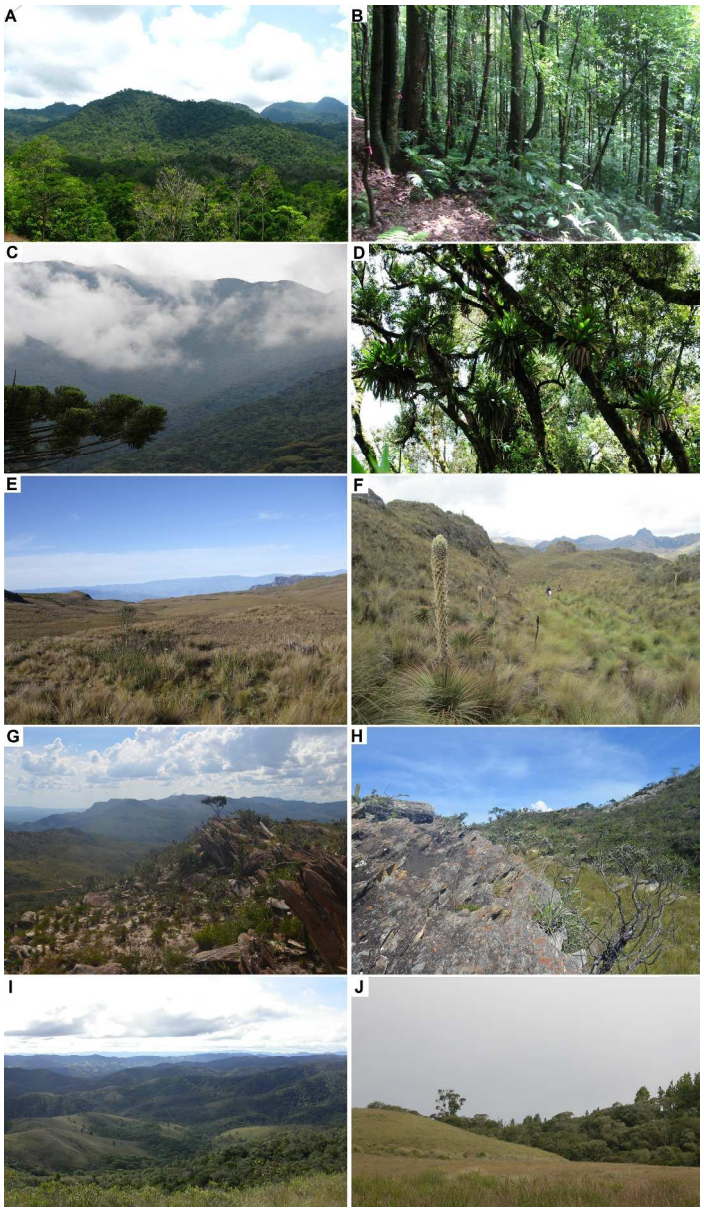

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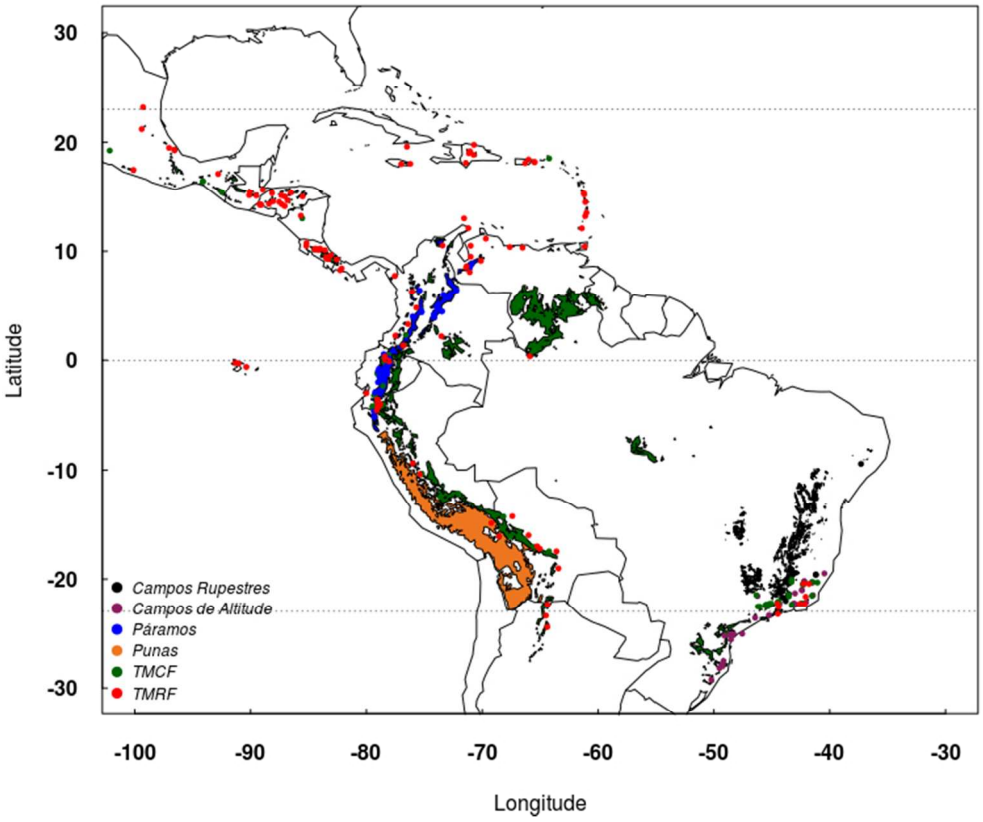

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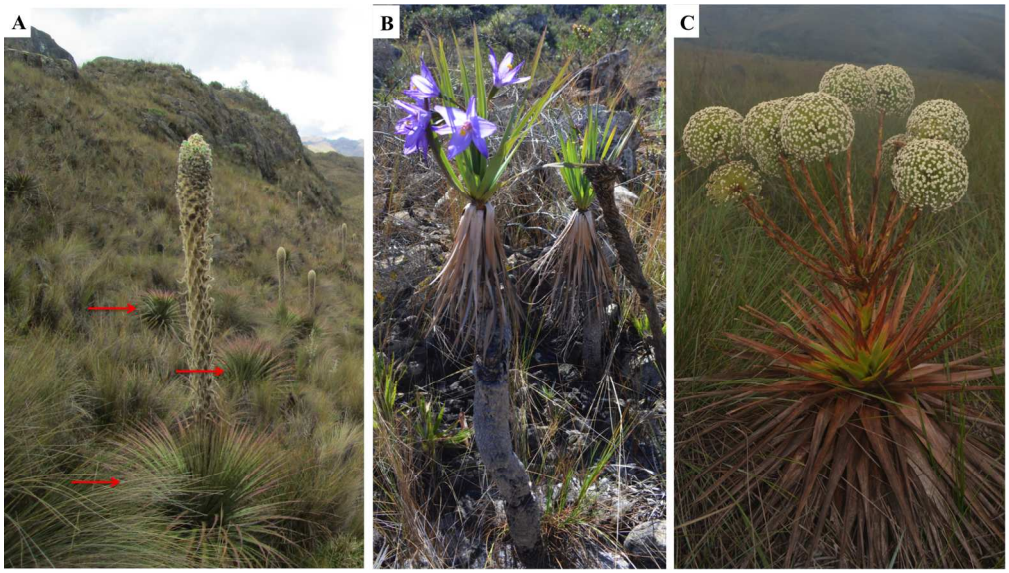

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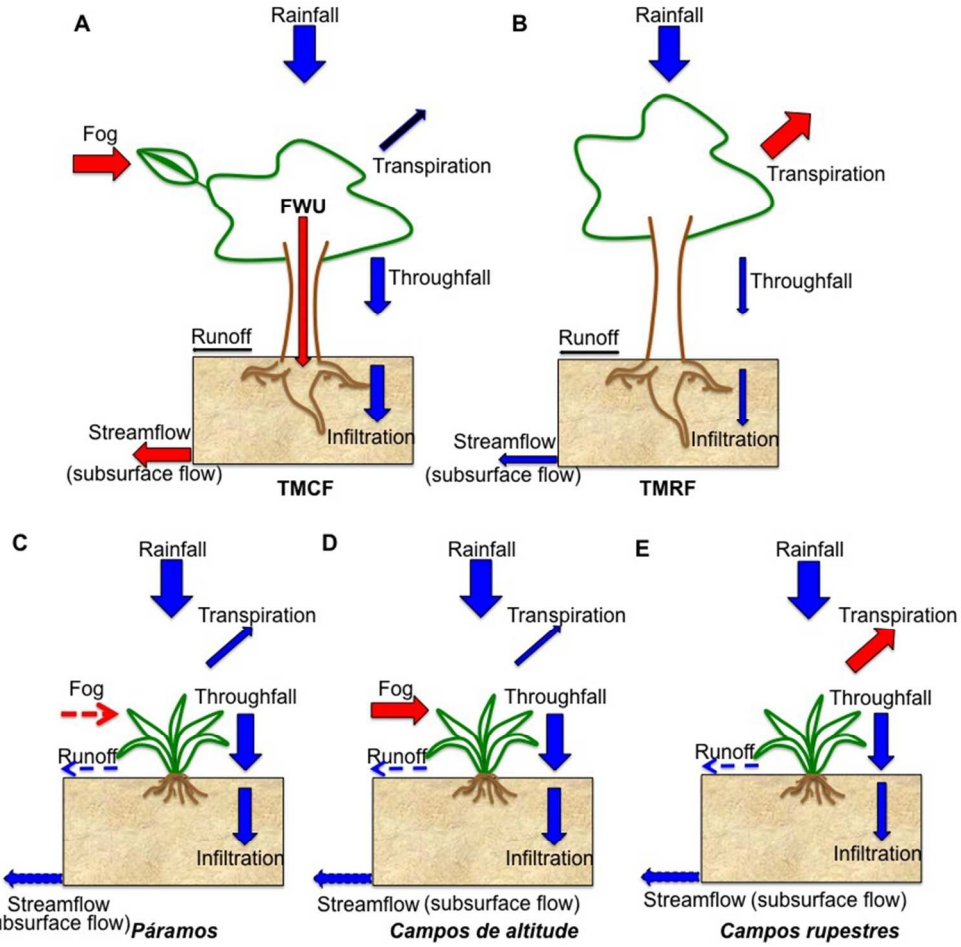

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